

## IN THIS ISSUE

Over the last couple of centuries, vast tracts of natural communities have been converted to human use for agriculture, housing, industrial uses, and otherwise. Only in recent decades has a largescale effort been made to reclaim lost habitats by restoration activities, and this journal has published several articles on restoration in recent years. A related, though also important, process is that of regeneration of tree species for commercial harvest. The first article in the current issue is an exploration of the possibility of using mature pine plantations in southern Michigan as a site for the restoration of oaks. This is necessary, because it has proven difficult for oak species to regenerate in existing oak forests, since the process of succession favors the replacement of oaks in natural communities by more shade-tolerant species, as well as the operation of several other factors enumerated in the article. The authors, Christian Tibaud, an undergraduate student at the time of this study, and David Rothstein, discuss in detail the reasons why mature pine plantations serve as a viable site for oak regeneration, report on their experimental plantings to confirm that these plantations are indeed a viable site for regeneration, and explain how such regeneration efforts can be managed for future success.

The second article in this issue is concerned with restoration efforts, in this case, the effect of latitudinal variation in seed sources for plantings used in restoration sites. Although conventional wisdom is that seeds should be sourced from areas near the restoration site, the authors posit that using more distantly sourced seeds may enhance the ability of the restored community to adapt to future climates and that using a mixture of seeds from various latitudes may enhance the evolutionary potential of the plants in the restoration. The authors, all of them experienced in plant conservation, examine the effect on phenology, pollination, and reproduction of common milkweed (*Asclepias syriaca*) in a common garden derived from three seed sources taken from a latitudinal gradient of 750 km in the Midwest and, based on their findings, discuss the advantages of mixed sourcing of seed sources for restoration efforts.

Two Noteworthy Collections articles follow. The first reports a new northward record for *Aphyllon riparium* (= *Orobancha riparia*) in Indiana, a species which has only recently been distinguished from the more common *A. ludovicianum*. The paper distinguishes the two species on both morphological and ecological grounds and also discusses the nomenclatural history and wider distribution of *A. riparium*. The second reports a moss species new to Wisconsin, *Paludella squarrosa*, along with a detailed description of the site, including both vascular and bryophyte associated species. The listing of bryophyte species at the site results in the report of 20 new county records for Oconto County.

Finally, Charlotte Gyllenhaal reviews *Braiding Sweetgrass* by Robin Wall Kimmerer, a book that has garnered much attention in recent years by botanists and others interested in the natural world and that has sparked interest in indige-

nous approaches to and relationships with the natural world, specifically through stories of several plant species.

————Michael Huft

**REVIEWERS FOR 2023 AND 2024**

I wish to thank the following people who reviewed manuscripts during 2023 and 2024 for *The Great Lakes Botanist*. Their comments were important, both to the authors and to the editor, and their efforts, which are essential to maintaining the high quality of the journal, are greatly appreciated.

- |                      |                   |
|----------------------|-------------------|
| Susan Fawcett        | Cyrus Nielsen     |
| Art Gilman           | Noel Pavlovic     |
| Janice Glime         | Michael Penskar   |
| Alex Graeff          | Anton A. Reznicek |
| Charlotte Gyllenhaal | Michael Rotter    |
| Riley Jackson        | J. Dan Skean, Jr. |
| Emmet Judziewicz     | Brad Slaughter    |
| Dan Kashian          | Julia Sosin       |

————Michael Huft

## RETROSPECTIVE BY THE OUTGOING EDITOR

This is my last issue as editor of *The Great Lakes Botanist*. I have served as editor for 12 volumes, volumes 52 through 63. During that time I have been privileged to read and edit scores of articles on many topics from many contributors from throughout the area served by the journal and beyond and have learned much from all of them. It has been an enjoyable journey, and through it I have met many colleagues I would not otherwise have had to opportunity to be in contact with.

The journal has gone through a number of changes during the past twelve years. The most significant is the change in name from *The Michigan Botanist*, the original name of the journal when it began publishing in 1962, to *The Great Lakes Botanist*. The change reflects what has always been the focus of the journal, which, from the beginning, has published articles on botanical matters from all of the states and provinces in the western Great Lakes region. It is the hope, however, that we will also be able to attract articles concerning botanical matters throughout North America north of Mexico. There have been smaller changes in format—for example, of the table of contents and of the Noteworthy Collections articles. Finally, the look and feel of the online version of the journal has been modernized.

I want to thank the many people who contribute to the success of *The Great Lakes Botanist*. First are the members of the Editorial Board, most recently, Tony Reznicek, Dan Kashian, Dan Skean, Mike Penskar, and Mike Rotter. Earlier members who are no longer on the board are Alan Prather, Anna Monfils, Tim Evans, and Catherine Yansa. All have served as a valuable sounding board as well as acting as external reviewers. Our typesetter, Susan Kenyon, has provided outstanding service in turning the raw material of the articles, including illustrations and tables, into a publishable format and has been our liaison with the printing company, Cushing-Malloy in Ann Arbor. The many external reviewers have provided invaluable commentary on articles within their expertise. The board of the Michigan Botanical Society, which is the owner and publisher of the journal, has consistently provided support, as have the chapters and members of the Society. I also thank our online host, Michigan Publishing, a division of the University of Michigan Library, which makes the journal's content available online, as well as the Hanes Fund, a nonprofit granting entity that funds our online presence. Most important, however, it is the many contributors, who by submitting excellent and varied articles, noteworthy collection notes, and book reviews, have made this journal the excellent publication that it is.

I am very happy now to turn the editorial tasks over to the new editor, Anton A. ("Tony") Reznicek, who I am confident will continue to insure the excellence of this journal. Tony is highly qualified, having been a member of The Michigan Botanical Society since the 1960s and having served as the journal's business manager for twelve years under its first editor, Edward G. Voss. Over the years he has generously provided advice and counsel to the editors, has been the

source of valuable historical perspective, and has contributed articles, reviews, and other items to the journal. He has spent his entire professional career at the University of Michigan, where he is now emeritus curator of the University Herbarium and where he continues his research in the Cyperaceae, especially the giant genus *Carex*, and in the floristics of Michigan and the greater western Great Lakes region, of which he is a pre-eminent authority.

Historically, the business end of *The Great Lakes Botanist* has been in the hands of a separate business manager who handles the finances, the subscription matters, and related items for the journal. However, during my tenure as editor, I have also filled the role of business manager. Now, I am pleased to pass those duties on to the very capable hands of Abigail (“Abbie”) Bristol, a member of the Southwest Chapter of The Michigan Botanical Society who also serves as the Invasive Species Management Coordinator for the Conservation District of Van Buren County, Michigan.

I look forward with confidence to the continued success of *The Great Lakes Botanist* and offer my very best wishes and congratulations to the new team.

——Michael Huft  
mhuft@att.net

## MATURE PINE PLANTATIONS AS POTENTIAL SITES FOR OAK REGENERATION IN PARKS AND NATURAL AREAS OF SOUTHERN MICHIGAN

Christian Tibaudo<sup>1</sup> and David Rothstein

Department of Forestry  
Michigan State University  
480 Wilson Road  
East Lansing, MI, 48824

### ABSTRACT

Poor regeneration of oak species (genus *Quercus*) is a widespread problem throughout the eastern United States. Recent research on forests managed for timber in northern Michigan has indicated that Civilian Conservation Corps (CCC) era pine (genus *Pinus*) plantations may provide better sites for oak regeneration than forests currently dominated by an oak overstory. Although not widely recognized, pine plantations were also established in southern Michigan during the same period and tend to reside on state and county parks managed primarily for conservation and recreation. We set out to determine the extent of pine plantations on three large public recreation areas in southern Michigan and to assess their potential as sites for oak regeneration. First, we analyzed aerial imagery to assess the proportion of upland areas occupied by planted conifer stands (including those dominated by pines). Next, we visited a sample of pine stands and adjacent upland oak forests to ground-truth our cover type classification and to assess the status of oak regeneration. We estimated there to be 147 ha of planted conifers in Waterloo State Recreation Area (3.2% of total upland forest area), 97 ha of planted conifers in Island Lake State Recreation Area (9.5% of total upland forest area), and 14 ha of planted conifers in Lake Lansing Park North (15.7% of total upland forest area). The plantations encountered varied in composition, but in general were dominated by either white pine (*Pinus strobus* L.) or red pine (*Pinus resinosa* Ait.). Other conifer species such as jack pine (*Pinus banksiana* Lamb.), scotch pine (*Pinus sylvestris* L.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were occasionally present. One large stand of Norway spruce (*Picea abies* (L.) H. Karst.) was also encountered. Oak seedling and sapling densities were similar and did not statistically differ between pine plantations and adjacent oak forest. Additionally, oak seedlings were significantly taller under planted pine than under oak forest, suggesting that these plantations provide better conditions for growth and recruitment into larger size classes. Together our results suggest that mature pine plantations in southern Michigan could be a focal point for managers seeking to promote oak regeneration.

KEYWORDS: oak regeneration; pine plantations; restoration; natural areas

### INTRODUCTION

Historically, oaks (genus *Quercus*) comprised an important component of the eastern US landscape (Loftis 1992). Oaks have tremendous economic value for their desirable timber, but also have great ecological value as a food source for mammals and birds. Increases in disturbance following European colonization, such as logging and subsequent fires, likely increased the dominance of oaks

---

<sup>1</sup> Author for correspondence (tibaudo@msu.edu)



across the landscape (Loftis 1992; Nowacki and Abrams 2008; Whitney 1987). Oak forests that exist today as a result of those disturbances are not returning to their former composition and are instead being replaced by more shade-tolerant competitors, such as red maple (*Acer rubrum* L.) (Nowacki and Abrams 2008; Fei et al. 2011; Knott et al. 2019). Many factors have been proposed as contributing to these failures in oak regeneration, including the reduced frequency of disturbance events, the increased presence of competitive seed sources, frost damage, deer browsing (Granger et al. 2018), and excessive shade from understory competitors (Hartman et al. 2005). Of particular concern is the apparent bottleneck between seedling and sapling size classes for oaks such that there is a dearth of sapling-size oaks able to recruit into the canopy as mature oak trees die (Crow 1988; Abrams 2003; Fei et al. 2005).

Whereas forest managers have for decades struggled to regenerate oaks in existing oak forests, several studies have shown that oaks are able to regenerate and recruit into sapling sizes much more readily under a pine (genus *Pinus*) canopy than under an oak canopy (Zhou et al. 1998; Hartman et al. 2005; Granger et al. 2018; Vander Yacht et al. 2022). Several factors have been proposed to explain improved growth and survival of oak seedlings and saplings under a pine canopy, including: (1) greater light transmission through the needle-leaved canopy (Buckley et al. 1999), (2) year-round frost protection from the evergreen canopy (Buckley et al. 1998), and (3) greater colonization of oak seedlings by beneficial ectomycorrhizal fungi (Zhou et al. 1998). Evidence for greater success of oak regeneration and recruitment under pine has led to recommendations to focus efforts on regenerating new oak stands on areas currently in mature pine plantations (Granger et al. 2018; Vander Yacht et al. 2022). Such an approach makes great sense for state and federal forestlands actively managed for timber in northern Michigan, Wisconsin, and Minnesota where red pine (*Pinus resinosa* Ait.) plantations cover over 600,000 hectares, a legacy of red pines being extensively planted across the region in the 1930s as part of the restoration efforts of the Civilian Conservation Corps (CCC) (Gilmore and Palik 2006). Because these 90+ year-old plantations are nearing maturity and final harvest, there exists a great opportunity to use them as a resource for oak regeneration on working forests managed by state and federal agencies.

Although CCC-era pine plantations are mostly associated with state and federal forest lands of northern Michigan, we have frequently encountered mature pine plantations from this era in forested parklands of southern Michigan, and in fact several studies from Ohio document the widespread occurrence of pine plantations established on abandoned agricultural lands in the 1930s and 1940s (Artigas and Boerner 1989; Abella 2010). Public lands in the southern portion of the Lower Peninsula occur in the heart of the oak–hickory forest region (Albert et al. 2014) and are managed for recreation and conservation rather than for timber (MDNR 2012a, 2012b). In this study we sought to assess both the prevalence of mature pine plantations in forested recreation areas in southern Michigan, as well as their suitability as sites for oak restoration efforts.

## MATERIALS AND METHODS

We assessed the extent of pine plantations and their suitability for oak regeneration in three large, forested recreation areas in the southern Lower Peninsula of Michigan. Waterloo Recreation Area (8000 ha) located between Jackson and Ann Arbor, Michigan and Island Lake State Recreation Area (1600 ha) located just southeast of Brighton, Michigan are large tracts managed by the Parks and Recreation Division of the Michigan Department of Natural Resources (MDNR) and are managed for both recreation and preservation of natural and cultural resources (MDNR 2012a and 2012b). Lake Lansing Park North just east of Lansing, Michigan is a 214-ha forested park managed as a natural recreation area by the Ingham County Parks Department. Uplands of all three parks are dominated by glaciofluvial landforms including outwash and ice-contact terrain, and all have excellent representation of oak-dominated Dry Southern Forest and Dry-Mesic Southern Forest natural communities as defined in Albert et al. (2014).

To estimate the areal extent of conifer plantations we digitized areas of evergreen cover within the park boundaries from 1998 Digital Orthophoto Quadrangle aerial imagery in ArcGIS Pro (version 3.0.2). We also used our GIS to create a layer of upland habitat by excluding any areas classed as wetlands or lakes or within 10 m of a stream according to the National Wetlands Inventory (U.S. Fish & Wildlife Service 2005), as well as any areas classed as open land, roads or development. We then calculated the total area classed as upland conifer within each park and expressed this as a proportion of the total area of upland forest habitat within each park.

We sorted contiguous stands of evergreen cover identified in our analysis of aerial imagery into three different area classes and then randomly selected stands from within these area classes for ground truthing and sampling of oak regeneration and recruitment. Sampling within these stands was conducted on a systematically arranged 80 × 80 m grid. Sampling effort differed by the area class, with the smallest stands (<1.62 hectares) receiving one centralized sample point, the next largest stands (1.62–6.1 hectares) receiving up to three systematically spaced points, and the largest stands (>6.1 hectares) receiving up to 10 systematically spaced points. For each sampled conifer stand, we identified an adjacent upland hardwood stand of equivalent area using aerial imagery. We arranged upland deciduous sample points on the same systematic sampling frame utilized for the samples in the pine plantations.

We navigated to our predetermined sampling points using a handheld GPS, where we measured the overstory composition, understory composition, and seedling layer oak regeneration. To characterize the overstory we used a 10-BAF (basal area factor) point sample from our sampling point, including only stems greater than 10 cm in diameter at breast height (DBH). To characterize the understory layer, we laid out a 6-m radius (0.11 ha) circular plot with our sampling point as the center and recorded any stems > 1.37 m high but < 10 cm DBH. Understory stems were tallied and recorded by species and 2.5 cm DBH size classes. For oak seedling measurements, we used three 2-m by 6-m belt transects originating at the sampling point and oriented at 0-, 120-, or 240-degree azimuths. Within these transects we counted and recorded the height of all oak seedlings. Because of challenges in distinguishing black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), and their hybrids in young seedlings and mature trees from bark alone, upland oaks were identified as either *Q. rubra/velutina* or white oak (*Q. alba* L.).

In order to assess the effects of forest cover type (pine plantation vs. natural hardwood) on oak regeneration and recruitment we used linear mixed-effects models with cover type as our main fixed effect and stand nested within park as a random effect. Response parameters included oak seedling density, oak sapling density, and mean height of oak seedlings. Reported p-values are derived from F-tests based on Satterwaite's method using the "lmerTest" package in R. All statistical analyses were conducted with RStudio version 4.3.2 (2023-10-31).

## RESULTS

Our GIS analysis revealed 147 ha of conifer plantation at Waterloo State Recreation Area (3.2% of the total upland forest area of the park), 97 ha of conifer plantation at Island Lake State Recreation Area (9.5% of the total upland

forest area of the park), and 14 ha of conifer plantation at Lake Lansing Park North (15.7% of the total upland forest area of the park). Across all three parks these conifer plantations occurred as patches within a larger matrix of surrounding hardwood forests (Figure 1). Detailed data on the composition of conifer plantations and native hardwood forests across the three parks are presented in Table 1. Red pine, white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) were the most dominant and frequently encountered species in conifer plantations with minor contributions from Scotch pine (*Pinus sylvestris* L.), jack pine (*Pinus banksiana* Lamb.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Groundtruthing data indicated the presence of planted conifers (whether pines or other evergreen conifers) in all areas identified as conifer plantations from aerial imagery, with average conifer relative dominance (percentage of total stand basal area) of 76%, 65%, and 73% in Waterloo, Island Lake and Lake Lansing parks, respectively. Northern red oak and black oak dominated the overstory of the upland hardwood forests across all three parks. White oak, red maple, and black cherry (*Prunus serotina* Ehrh) were consistent, but smaller, contributors to overstory basal area across all three parks. Big-tooth aspen (*Populus grandidentata* Michx.) was locally important at Lake Lansing Park North. Across all three parks, stocking was about 25% higher in the planted conifer stands compared to the adjacent hardwood stands, as indicated by basal area measurements (Table 1). The Norway spruce plantations encountered at Waterloo and Lake Lansing were clearly distinct from pine-dominated plantations in terms of casting a deep shade, such that we encountered zero regeneration by oaks and very little regeneration of any hardwoods in these stands. Therefore, we excluded pure Norway spruce plantations from our subsequent analyses and focused solely on pine plantations for the remainder of this study.

Oak seedling density in pine plantations and native oak forests across all the parks is shown in Figure 2. Overall, there was no statistically significant difference in oak seedling density between pine plantations and native oak forests ( $p = 0.365$ ), although patterns in the data varied across the parks. Oak seedling density tended to be greater at Island Lake State Recreation Area and lower overall at Lake Lansing Park North and Waterloo State Recreation Area.

In contrast to oak seedling density, there was a statistically-significant effect of cover type on oak seedling height ( $p = 0.017$ ), whereby oak seedlings were much taller under pine plantations than they were under native oak forest canopy (Figure 3). Note that because all but two oak forest plots at Waterloo had zero oak seedlings, we confined our analysis of seedling heights to Island Lake and Lake Lansing parks. This pattern was pronounced and consistent across the two parks, with oak seedlings growing under an oak canopy rarely exceeding 20 cm in height (Figure 3). Finally, there was no statistically significant difference in oak sapling density between pine plantations and native oak forests ( $p = 0.340$ ) (Figure 4). Oak saplings were almost entirely absent from either cover type at Lake Lansing Park North, whereas they were more common at the other two parks (Figure 3).



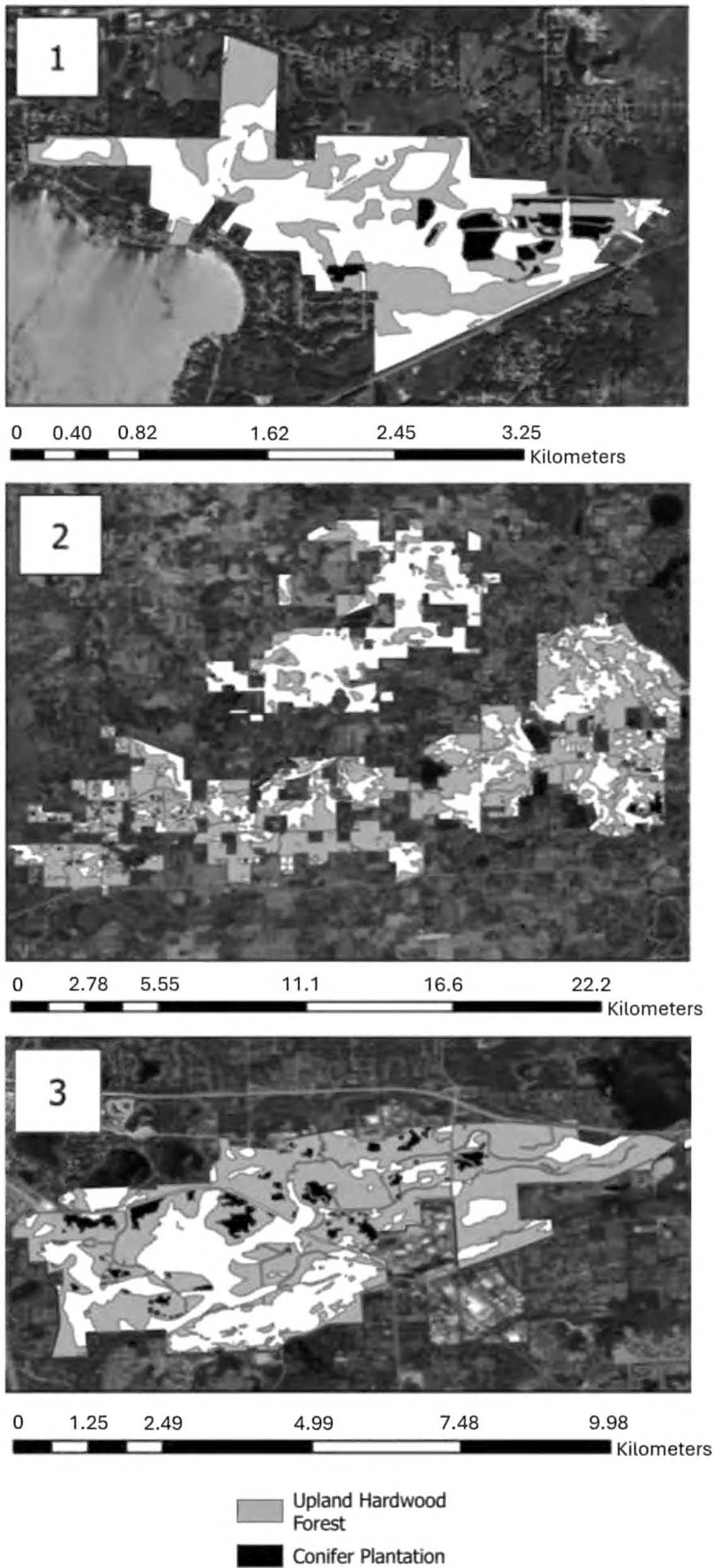


FIGURE 1. Upland forest cover of Lake Lansing Park North (1), Waterloo State Recreation Area (2), and Island Lake State Recreation Area (3). In Panels 1, 2, and 3 upland hardwood forests are mapped in grey, conifer plantations in black, and all excluded wetlands, open lands and developed areas in white.

TABLE 1. Overstory basal areas (m<sup>2</sup> per ha) from ground truthing plots located in areas predicted to be planted conifers (Plantation) vs natural hardwood stands (Hardwood) from aerial imagery. Data are means for each species within each classified forest type with ranges given in parentheses.

	Waterloo		Island Lake		Lake Lansing	
	Plantation	Hardwood	Plantation	Hardwood	Plantation	Hardwood
<b>Conifers</b>						
<i>Picea abies</i>	13 (0–53)	0 (0–0)	0 (0–0)	0 (0–0)	12 (0–48)	0 (0–0)
<i>Pinus banksiana</i>	0 (0–0)	0 (0–0)	1 (0–6)	0 (0–0)	2 (0–9)	0 (0–0)
<i>Pinus resinosa</i>	6 (0–20)	0 (0–0)	18 (0–41)	1 (0–5)	8 (0–24)	0 (0–0)
<i>Pinus strobus</i>	14 (0–34)	3 (0–6)	7 (0–29)	1 (0–5)	5 (0–18)	0 (0–0)
<i>Pinus sylvestris</i>	0 (0–0)	0 (0–0)	1 (0–8)	0 (0–0)	3 (0–9)	0 (0–0)
<i>Pseudotsuga menziesii</i>	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	2 (0–14)	0 (0–0)
<b>Hardwoods</b>						
<i>Acer rubrum</i>	1 (0–4)	2 (0–5)	1 (0–3)	2 (0–8)	2 (0–3)	4 (1–7)
<i>Carya glabra/ovata</i>	0 (0–0)	1 (0–1)	0 (0–2)	0 (0–2)	0 (0–0)	1 (0–2)
<i>Quercus alba</i>	0 (0–1)	2 (0–5)	0 (0–0)	2 (0–6)	1 (0–5)	2 (0–7)
<i>Quercus rubra/velutina</i>	4 (1–9)	23 (17–29)	4 (1–13)	19 (11–27)	4 (0–16)	13 (2–29)
<i>Populus grandidentata</i>	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	11 (0–37)
<i>Prunus serotina</i>	3 (0–5)	2 (0–5)	3 (0–7)	2 (0–6)	2 (1–4)	5 (0–9)
<i>Ulmus americana</i>	0 (0–0)	0 (0–0)	1 (0–3)	0 (0–1)	0 (0–1)	0 (0–1)
Other native trees <sup>1</sup>	1 (0–2)	2 (1–3)	2 (0–6)	1 (0–5)	0 (0–1)	1 (0–3)
<b>Total Stand Basal Area</b>	<b>44 (26–57)</b>	<b>36 (30–41)</b>	<b>37 (25–51)</b>	<b>29 (21–40)</b>	<b>44 (14–55)</b>	<b>38 (30–46)</b>
<b>% BA in Conifers</b>	<b>76 (64–95)</b>	<b>5 (0–11)</b>	<b>65 (14–93)</b>	<b>5 (0–18)</b>	<b>73 (52–89)</b>	<b>0 (0–1)</b>

<sup>1</sup>Includes: *Acer negundo* L., *Acer saccharinum* L., *Acer saccharum* Marsh., *Amelanchier* spp., *Carpinus caroliniana* Walter, *Cornus florida* L., *Elaeagnus umbellata* Thunb., *Fagus grandifolia* Ehrh., *Juglans nigra* L., *Juniperus virginiana* L., *Malus* spp., *Ostrya virginiana* (Mill.) K. Koch, *Populus tremuloides* Michx., *Rhamnus cathartica* L., *Robinia pseudoacacia* L., *Sassafras albidum* (Nutt.) Nees, *Tilia americana* L.

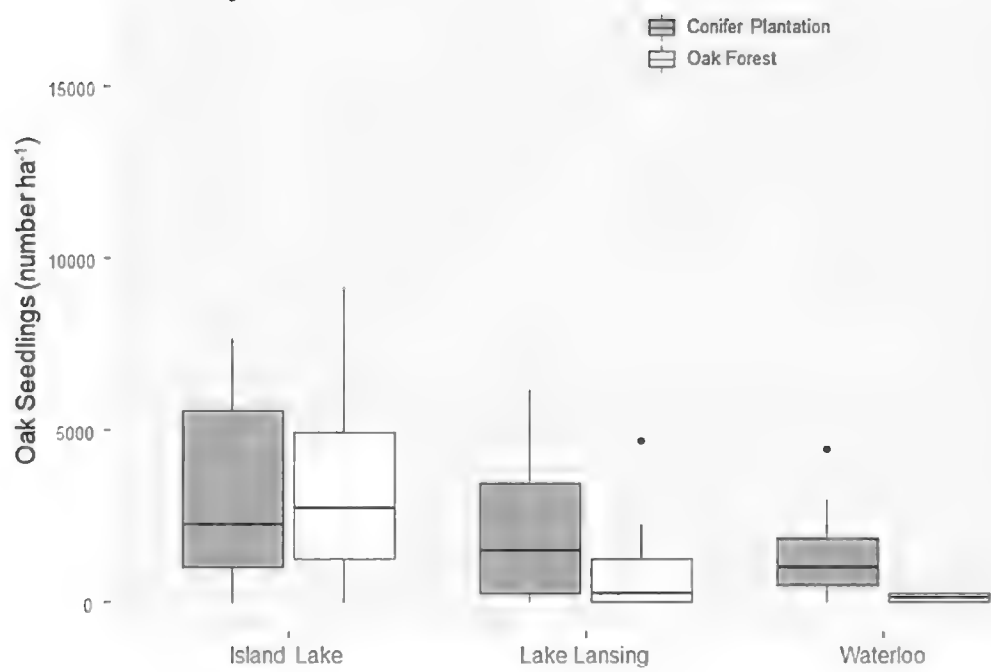


FIGURE 2. Oak seedling density under conifer plantation vs. oak forest across the three southern Michigan parks. In the box-and-whiskers diagram the horizontal black line represents the median, the box represents the middle 50th percentile of data. Upper and lower 25th percentiles are represented by the whiskers, and outlying data are shown as black dots.

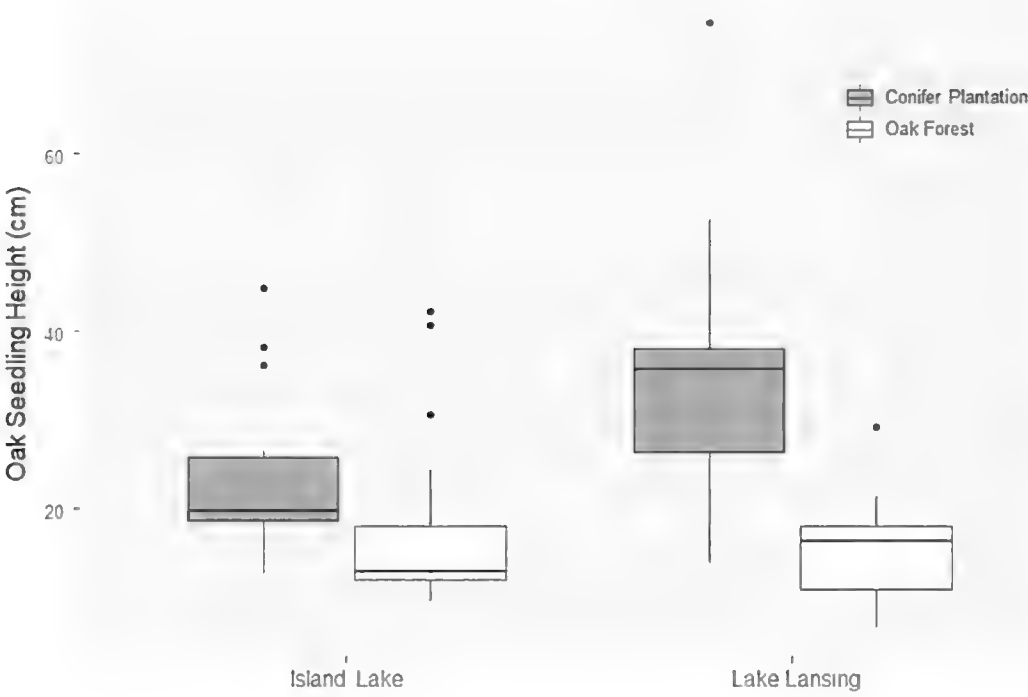


FIGURE 3. Average height of oak seedlings in plots under conifer plantation vs. oak forest at Island Lake State Recreation Area and Lake Lansing Park North. Data representation for the box-and-whiskers diagrams are as described in the caption for Figure 2.

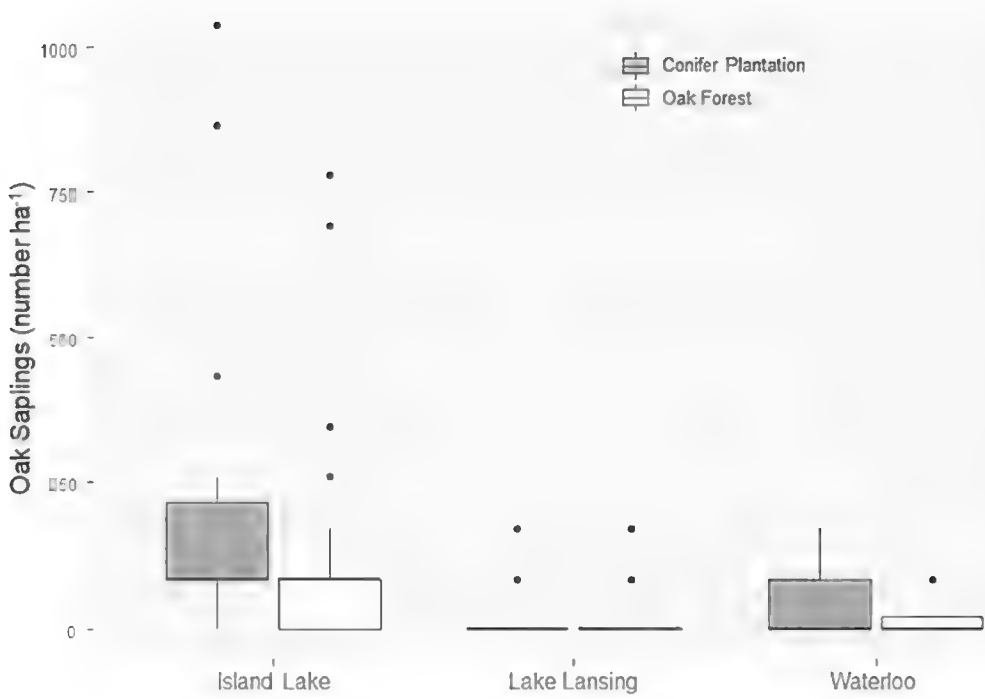


FIGURE 4. Oak sapling density under conifer plantation vs. oak forest across the three southern Michigan Parks. Data representation for the box-and-whiskers diagrams are as described in the caption for Figure 2.

## DISCUSSION

Results from our assessment of oak regeneration across these parks are consistent with, and provide further support for, a growing body of research showing that environmental conditions underneath a pine canopy are more conducive to the growth and survival of oak seedlings compared to conditions beneath an oak canopy (Zhou et al. 1998; Hartman et al. 2005; Granger et al. 2018; Vander Yacht et al. 2022). Initially, our finding of no statistically-significant difference in oak seedling density between pine plantations and surrounding oak forests would seem to indicate no difference in suitability for oak regeneration between these two habitats. However, when we consider the fact that seedling densities at any given time reflect the demographic balance between inputs of new germinants and outputs from seedling mortality or growth into the sapling layer, we argue that these data are actually suggestive of more favorable conditions for oak seedlings under pine plantations. Because the vast majority of seeds fall within a short distance of the parent tree, especially for heavy seeded species such as oaks (Sork 1984; Clark et al. 1999; Hewitt and Kellman 2002), it is undoubtedly the case that the input of acorns to the seedbank is much greater in our oak-forest stands than within the pine plantations. Acorn inputs to our pine plantations likely result from infrequent long-distance animal dispersal events (Sork 1984; Hewitt and Kellman 2002; Vander Yacht et al. 2022). Therefore, if inputs of new germinants are greater under an oak canopy than under pines, then the equivalent seedling densities must arise from lower seedling mortality under pines, faster growth out of the seedling layer under pines, or a combination of both.

Because we did not harvest and age seedlings, we cannot with confidence distinguish the importance of lower mortality vs faster seedling growth under pines. However, a few lines of evidence suggest that differences in mortality are likely to be the most important. First, studies of oak seedling demography in forest understories consistently show very high rates of mortality with most established oak seedlings only surviving for a few years (Royse et al. 2010; Brose and Rebbeck 2017; Cleavitt et al. 2023). Furthermore, oak seedlings that do survive tend to grow very slowly and can remain in the seedling layer for decades (Cleavitt et al. 2023). Together with the equivalent densities of saplings under oak vs pine canopies (Figure 4), this suggests that differences in seedling mortality are likely the driving difference between cover types. Thus we speculate that the equivalent densities of taller seedlings under pine plantations, combined with likely greater inputs of acorns in oak stands, suggests that oak seedlings are establishing regularly within our oak stands but are turning over rapidly due to high mortality. We rarely encountered oak seedlings greater than 20 cm in height in oak forests, indicating little potential for growth and recruitment into the sapling layer under an oak canopy. In contrast, under pine plantations with lower rates of acorn inputs, the equivalent seedling densities and much larger seedling heights suggests more favorable conditions for oak seedling survival, growth, and potential recruitment into the sapling layer.

Although the underlying mechanisms remain poorly understood, our data add to a growing number of studies indicating improved performance of oak seedlings under a pine canopy compared to their performance under an oak



canopy (Zhou et al. 1998; Hartman et al. 2005; Granger et al. 2018; Vander Yacht et al. 2022). Mature pine plantations were present across all three of the southern Michigan parks we surveyed and ranged from a low of 3% to a high of 16% of the upland forestland of these parks. Based on the size and conditions of trees in these plantations, they all likely originated in the mid-20th century, presumably as part of efforts to reforest abandoned agricultural land that were active across the state from the 1930s to the 1950s (Dickman and Leefers 2016). Although these 20th century reforestation efforts are most often associated with the state and federal forest lands in the north (Gilmore and Palik 2006), reforestation efforts were also occurring in southern Michigan (Dickman and Leefers 2016). The fact that we found these plantations distributed across all three parks that we studied suggests that they may occur in similar parks and natural areas throughout the southern portions of the state, and even in neighboring states of Ohio, Indiana, and Wisconsin (e.g., Abella 2010).

Although these plantations made up a small percentage of the total forested area, we argue that they still warrant attention by managers of these parks (and similar ones across the region) as sites on which to focus effort towards oak regeneration and habitat restoration. The most abundant plantation conifers we encountered (red pine and white pine) are both native components of the regional flora; however, their occurrence in pure stands represents a wide divergence from the native ecosystems of this region (Albert et al. 2014), and there is an interest in opportunities to transition these highly artificial systems to more site-appropriate plant communities (Artigas and Boerner 1989; Abella 2010; Palik and Kastendick 2023). Over the coming decades we can expect to see increasing levels of pine mortality in these mature plantations, especially for shorter-lived species such as Scotch pine and jack pine, and successional transitions to hardwood dominated systems (Artigas and Boerner 1989). The emerging evidence of improved performance of oak seedlings under pine canopies suggests that restoration efforts targeted at promoting oak recruitment into the large sapling layer under the existing pine canopies could guide these transitions toward a more desirable outcome. In contrast, leaving these mature plantations to their own devices may result in continuing shifts towards more mesophytic shade-tolerant species, such as red maple (Nowacki and Abrams 2008). We recommend that managers experiment with planting oak seedlings in mature pine plantations as well as protecting existing and newly planted seedlings from deer. Deer browsing is a major constraint against oak regeneration (Redick and Jacobs 2020), and we consistently observed evidence of deer browse on oak seedlings under both pine and oak canopies across our study sites. If oak seedlings grow faster under a pine canopy, then deer protection during recruitment of oaks from seedling to sapling layers will likely take less effort and expense than under an oak canopy.

#### AUTHOR CONTRIBUTIONS

CT and DR collaborated on the conception and design of the study. CT carried out the field sampling and data analysis and wrote the initial draft of the manuscript. DR supervised field sampling and data analysis and revised the initial draft for submission.

## ACKNOWLEDGMENTS

We gratefully acknowledge financial support provided to C. Tibaudo for this project by the Provost's Undergraduate Research Grants distributed through the College of Agriculture and Natural Resources at Michigan State University. D. Rothstein was supported by a USDA-NIFA McIntire Stennis Capacity Grant (Award # MICL06006).

## LITERATURE CITED

- Abella, S. R. (2010). Thinning pine plantations to reestablish oak openings species in northwestern Ohio. *Environmental Management* 46: 391–403.
- Abrams, M. D. (2003). Where has all the white oak gone? *BioScience* 53: 927–939.
- Albert, D. A., B. S. Slaughter, M. A. Kost, and J. G. Cohen. (2014). A field guide to the natural communities of Michigan. Michigan State University Press, East Lansing.
- Artigas, F. J., and R. E. Boerner. (1989). Advance regeneration and seed banking of woody plants in Ohio pine plantations: Implications for landscape change. *Landscape Ecology* 2: 139–150.
- Buckley, D. S., T. L. Sharik, and J. G. Isebrands. (1998). Regeneration of northern red oak: Positive and negative effects of competitor removal. *Ecology* 79: 65–78.
- Brose, P. H., and J. Rebbeck. (2017). A comparison of the survival and development of the seedlings of four upland oak species grown in four different understory light environments. *Journal of Forestry* 115: 159–166.
- Buckley, D. S., J. G. Isebrands, and T. L. Sharik. (1999). Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *Northern Journal of Applied Forestry* 16: 25–32.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. (1999). Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80: 1475–1494.
- Cleavitt, N. L., J. J. Battles, J. H. Matthes, and S. Wentzell-Brehme. (2024). Multi-cohort survival of northern red oak seedlings at a northern hardwood forest transition. *Ecosphere* 15: e4949.
- Crow, T. R. (1988). Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—A review. *Forest science* 34: 19–40.
- Dickmann, D. I., and L. A. Leefers. (2016). The forests of Michigan. The University of Michigan Press, Ann Arbor.
- Fei, S., P. J. Gould, K. C. Steiner, J. C. Finley, and M. E. McDill. (2005). Forest regeneration composition and development in upland, mixed-oak forests. *Tree Physiology* 25: 1495–1500.
- Fei, S., N. Kong, K. C. Steiner, W. K. Moser, and E. B. Steiner. (2011). Change in oak abundance in the eastern United States from 1980 to 2008. *Forest Ecology and Management* 262: 1370–1377.
- Gilmore, D. W., and B. Palik. (2006). A revised managers handbook for red pine in the North Central region. USDA Forest Service General Technical Report NC-264, North Central Research Station, St. Paul, Minnesota.
- Granger, J. J., D. S. Buckley, T. L. Sharik, J. M. Zobel, W. W. DeBord, J. P. Hartman, J. G. Henning, et al. (2018). Northern red oak regeneration: 25-year results of cutting and prescribed fire in Michigan oak and pine stands. *Forest Ecology and Management* 429: 467–479.
- Hartman, J. P., D. S. Buckley, and T. L. Sharik. (2005). Differential success of oak and red maple regeneration in oak and pine stands on intermediate-quality sites in northern Lower Michigan. *Forest Ecology and Management* 216: 77–90.
- Hewitt, N., and M. Kellman. (2002). Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. *Journal of Biogeography* 29: 351–363.
- Knott, J. A., J. M. Desprez, C. M. Oswalt, and S. Fei. (2019). Shifts in forest composition in the eastern United States. *Forest Ecology and Management* 433: 176–183.
- Loftis, D. (1992). Oak regeneration: Serious problems, practical recommendations. Symposium Proceedings; Presented by the Center for Oak Studies. Asheville, North Carolina. Available at [https://www.srs.fs.usda.gov/pubs/gtr/gtr\\_se084.pdf](https://www.srs.fs.usda.gov/pubs/gtr/gtr_se084.pdf)
- MDNR. (2012a). Waterloo Recreation Area general management plan. Available at [https://www.michigan.gov/-/media/Project/Websites/dnr/Documents/PRD/MgtPlans/Waterloo\\_Phase1\\_GMP.pdf?rev=d9dbce765b8a40e6978d825dd666e0d5](https://www.michigan.gov/-/media/Project/Websites/dnr/Documents/PRD/MgtPlans/Waterloo_Phase1_GMP.pdf?rev=d9dbce765b8a40e6978d825dd666e0d5). (Accessed December 20, 2023).
- MDNR. (2012b). Island Lake Recreation Area General Management Plan. [https://www.michigan.gov/dnr/-/media/Project/Websites/dnr/Documents/PRD/MgtPlans/IslandLake\\_Phase-](https://www.michigan.gov/dnr/-/media/Project/Websites/dnr/Documents/PRD/MgtPlans/IslandLake_Phase-)

- 1\_GMP.pdf?rev=9ad16d53ddc74eba91f27d8b5ab9f025&hash=2C5359882BE3B0F36B6539460EBB1910. (Accessed December 20, 2023).
- Nowacki, G. J., and M. D. Abrams. (2008). The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58: 123–138.
- Palik, B. J., and D. N. Kastendick. (2023). Restoration of woody plant communities in red pine plantations on abandoned agricultural land in northern Minnesota, USA. *Forest Ecology and Management* 541: 121095.
- Redick, C. H., and D. F. Jacobs. (2020). Mitigation of deer herbivory in temperate hardwood forest regeneration: A meta-analysis of research literature. *Forests* 11: 1220.
- Royse, J., M. A. Arthur, A. Schörgendorfer, and D. L. Loftis. (2010). Establishment and growth of oak (*Quercus alba*, *Quercus prinus*) seedlings in burned and fire-excluded upland forests on the Cumberland Plateau. *Forest Ecology and Management*, 260: 502–510.
- Sork, V. L. (1984). Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. *Ecology* 65: 1020–1022.
- U.S. Fish & Wildlife Service. (2005). National Wetlands Inventory. Available at <https://www.fws.gov/program/national-wetlands-inventory/wetlands-mapper>. (Accessed September 20, 2022).
- Vander Yacht, A. L., R. K. Kobe, and M. B. Walters. (2022). Hardwood regeneration in red pine plantations: Thinning and site quality effects on changes in density and species composition from edges to interiors. *Forest Ecology and Management* 526: 120576.
- Whitney, G. G. (1987). An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology* 75: 667–684.
- Zhou, M., T. L. Sharik, M. F. Jurgensen, D. L. Richter, M. R. Gale, and T. D. Drummer. (1998). Regeneration of northern red oak in relation to ectomycorrhizae in oak and pine stands after overstory and understory manipulations. *Northern Journal of Applied Forestry* 15: 182–190.

## **LATITUDINAL VARIATION IN PHENOLOGY AND REPRODUCTION AMONG SEED SOURCES OF *ASCLEPIAS SYRIACA* L. (COMMON MILKWEED)**

Jessamine Finch<sup>1\*</sup>

Conservation Department, Native Plant Trust  
Framingham, Massachusetts 01701

Conservation & Research Department, Atlanta Botanical Garden  
Atlanta, GA 30309

Program in Plant Biology and Conservation  
Northwestern University  
Evanston, Illinois 60208

Negaunee Institute for Plant Conservation Science and Action  
Chicago Botanic Garden  
Glencoe, Illinois 60022

Imeña Valdes\*

Program in Plant Biology and Conservation  
Northwestern University  
Evanston, Illinois 60208

Negaunee Institute for Plant Conservation Science and Action  
Chicago Botanic Garden  
Glencoe, Illinois 60022

Kayri Havens

Negaunee Institute for Plant Conservation Science and Action  
Chicago Botanic Garden  
Glencoe, Illinois 60022

Program in Plant Biology and Conservation  
Northwestern University  
Evanston, Illinois 60208

### **ABSTRACT**

The value of ecological restoration is contingent on the appropriate sourcing of plant materials to establish a plant community and restore ecological function. Long-standing recommendations to source plants from close to the restoration site are now being complemented by strategies aimed at maximizing adaptation to future climates and evolutionary potential, such as including a greater variety of seed sources. However, intraspecific variation in phenology among seed sources may have direct effects on trophic interactions, including insect pollination. To investigate the effect of seed source on plant phenology, pollination, and reproduction, we compared three populations of *Asclepias syriaca* L. (common milkweed) collected along a 750 km latitudinal gradient in the Midwest

---

<sup>1</sup>Author for correspondence (jfinch@atlantabg.org)

\*These authors share first authorship



U.S. in a centrally located common garden grown for three years. Persistent phenological and phenotypic differences were found across multiple growing seasons. Plants from northern sources flowered earlier, were shorter at maturity, and demonstrated considerably less interannual variation in phenology than those from southern sources. Later flowering phenology, observed in plants from southern sources, was associated with increased floral visitation, increased number of viable fruits, and fewer aborted fruits than those from northern sources. These results suggest that plants from southern sources may perform better than locally-sourced plants or those from northern sources under restoration settings. In addition, populations may demonstrate decreased fruit production under climate change, with implications for population persistence and colonization of new sites. However, the use of assisted gene flow through the introduction of seed from southern populations could introduce adaptive phenological traits and expedite adaptation to changing climates. Additionally, these results suggest that the mixing of seed sources for restoration and habitat creation could greatly expand flowering windows with implications for pollinator conservation.

KEYWORDS: milkweed, seed source, provenance, phenology, climate change

## INTRODUCTION

Wild lands around the globe are facing numerous challenges from anthropogenic disturbance, invasive species, and pollution as well as from climate-related natural disasters like wildfire, drought, or floods. Ecological restoration, the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration International Science & Policy Working Group 2004), is becoming essential to maintain robust ecological communities, the biodiversity they support, and the ecosystem services they provide. As we begin the United Nations Decade on Ecosystem Restoration 2021–2030 (UNEP 2024), ecological restoration has become a high priority, as highlighted in numerous national—e.g., the Biden Administration’s “America the Beautiful Initiative”—(USDOI 2024) and international policy documents—e.g., the Global Strategy for Plant Conservation (CBD 2024), the Sustainable Development Goals (UN 2015), and the Bonn Challenge (IUCN 2020). Since the majority of restoration projects involve the introduction of seeds or seedlings, one of the ongoing challenges is determining a provenancing strategy for sourcing seeds or plant material to ensure it is well-adapted to the site (Broadhurst et al. 2008; Prober et al. 2015; Breed et al. 2018).

Local adaptation is well-documented in plants (Leimu and Fischer 2008; Hereford 2009), and the assumption that “local is best” has guided seed sourcing decisions for decades (Mortlock 2000; McKay et al. 2005). However, rapidly changing climate has led restoration practitioners to question these assumptions as local seed sources may be better adapted to historical or contemporary climates than to future ones (Broadhurst et al. 2008; Havens et al. 2015; Prober et al. 2015; Breed et al. 2018). Seed transfer zones (the areas from which germplasm can be moved and still be well-adapted to the climate) are influenced by many species-specific and site-specific factors, including patterns of gene flow, endemism, and the heterogeneity and stability of the landscape (Johnson et al. 2004; Havens et al. 2015). If restored populations are to survive projected future climates, seed transfer zones will need to become more dynamic (Kramer and Havens 2009). As the recognition of the need to prepare for future climates increases, several alternative strategies to local provenancing have been sug-

gested. These strategies generally either increase the genetic diversity of the source material (and therefore presumably the adaptive potential of the plants) or attempt to match seed source with anticipated future climate at a restoration site (Breed et al. 2018). Despite many years of robust discussion in the literature of the pros and cons of various provenancing strategies, which we understand can be challenging to implement in practice, empirical studies are still limited.

Central to the provenancing debate are not only the direct effects on the restoration related to the climatic fit of the plant material to the site, but also indirect effects on ecological function, including plant–animal interactions (Hobbs and Cramer 2008; Genes and Dirzo 2022). Plant phenology, as dictated by genetic and environmental variables, defines the temporal overlap and hence the potential for direct interaction across trophic levels (Durant et al. 2005; Peralta et al. 2020). Rapid anthropogenic climate change, including increases in mean temperature as well as in climate extremes and variability, has been linked to phenological shifts, such as earlier leaf out and flowering (Anderson et al. 2012; Piao et al. 2019). As species can respond independently to climatic shifts, there is a potential for plant–pollinator mismatch, or for divergent timing of flowering and pollinator life cycles, which can reduce fitness in plant and/or pollinator (Memmott et al. 2007; Forrest 2014; Howard 2018). Recent, expanded investigations of the impact of seed source have begun to document effects on species interactions and associated communities (Bucharova et al. 2016; Gehring et al. 2017; Gosney et al. 2017), including the relationship between plant phenology and pollinator networks (Bucharova et al. 2021). As restoration aims to reestablish interactions as well as organisms, an expanded understanding of the impact of seed source on plant performance and ecology is key to a comprehensive and resilient ecological restoration (Breed et al. 2018).

Since the relationship between seed source and pollinators are not one-way, but a mutualism, we would expect to see impacts on plant fitness and hence the successful establishment of a self-sustaining, restored plant community. To investigate the impact of seed source on plant phenology, pollination, and reproduction, we conducted a three-year common garden trial for *Asclepias syriaca* L. (common milkweed, Apocynaceae) within the core of its native range in the midwestern United States. This species is of particular relevance given its central role as a larval host in the life cycle of the imperiled *Danaus plexippus* L. (monarch butterfly), a charismatic pollinator species that has garnered international attention over the last decade (Brower et al. 2012; Trudeau et al. 2016; Thogmartin et al. 2017a). The study design allowed for a simultaneous test of interactions between seed source and pollinators as well as between seed source and climate, within which we tested four related hypotheses:

**H1 Flowering Phenology** – Flowering phenology varies among seed sources and follows source latitude, with northern sources flowering earlier than southern sources.

**H2 Floral Visitation** – Floral visitation varies among seed sources and mirrors flowering phenology, with increased floral visitation during peak flowering.

- H3 Plant Size** – Plant height at maturity varies among seed sources and follows source latitude, with northern sources reaching shorter maximum heights than southern sources.
- H4 Reproduction** – Fruit set varies among seed sources and follows source latitude, with northern sources generating less reproductive output than southern sources.

MATERIALS AND METHODS

Study Species

Milkweeds (*Asclepias* spp.) are characterized by a unique floral morphology and milky, alkaloid-rich latex that has driven coevolution with many insect herbivores, most famously the monarch butterfly, which depends on milkweed as a larva host plant to complete its lifecycle (Malcolm 1994). Over the last 20 years, dramatic declines have been observed in the overwintering size of the eastern migratory population of monarch butterflies in North America (Semmens et al. 2016). Monarch declines have been linked to a range of interrelated factors, including habitat loss, pesticide use, and climate change (Flockhart et al. 2014; Thogmartin et al. 2017b). In response there has been a marked increase in monarch habitat restoration efforts, including the recommendation to plant 1.8 billion stems of milkweed along their migratory route in the midwestern United States. (Pleasants 2017; Midwest Association of Fish and Wildlife Agencies 2018). Importantly, milkweed flowers lack an exposed stigmatic surface, preventing self-fertilization and requiring insect-mediated transfer of pollen packages (pollinia) through narrow floral openings called stigmatic slits. Plant species with obligate animal pollination syndromes, such as milkweeds, are expected to be more sensitive to changes in pollinator abundance and phenology as a result of climate change. Due to the wider interest in planting milkweed to bolster the monarch population, as well as its reproductive dependence on insect pollination, the relationship between seed source, phenology, and reproduction in milkweed was investigated. Specifically, common milkweed was studied, a generalist that thrives in marginal habitats, such as roadsides and agricultural field margins, which contributes to its status as one of the most abundant milkweed species in the upper Midwest (Hartzler and Buhler 2000). Results of stable isotope studies of overwintering monarch butterflies in Mexico support the assumption that common milkweed is one of the most important larval food sources (Seiber et al. 1986).

Seed Collection and Common Garden

In fall 2013, seed was collected from three naturally occurring populations of common milkweed in Minnesota, Illinois, and Missouri (Table 1). Seed collections were carried out at the time of seed dispersal with at least thirty individuals sampled per population. To maximize the likelihood of collecting from genetically distinct individuals, seeds were collected from stems spaced at least five meters apart. Seeds were cleaned manually by removing them from the pods and removing the comas. Seeds were then combined by source population. The seeds were germinated in production greenhouses at the Chicago Botanic Garden in Glencoe, Illinois in the winter of 2013–14. In spring 2014, a common garden was established at the Chicago Botanic Garden consisting of 144 individuals per seed source planted into a grid (24–30” spacing) to form three adjacent blocks (4.28 × 9.14m) following stratified random placement (42°08’36.4”N 87°47’09.4”W). In this context the Illinois seed source is considered to be local, with the Minnesota and Missouri sources considered to be northern

TABLE 1. Location of populations from which seeds were collected.

State	Location	Latitude (N)	Longitude (W)
Minnesota	Minnesota Landscape Arboretum, Bennett-Johnson Prairie	44° 51' 36"	–93° 37' 33.6"
Illinois	Nachusa Grasslands	41° 52' 51.6"	–89° 20' 31.2"
Missouri	Roadside, west of the intersection of I-44 and Missouri Hwy 141	38° 32' 16.8"	–90° 30' 7.2"

TABLE 2. Phenophase is defined for each umbel (inflorescence) and averaged across all umbels on the plant to determine plant phenophase. Reference photos are provided in Figure 1.

Phenophase	Description
Vegetative	No buds, flowers, or fruits present
Flower buds	Buds with green to light pink coloration, no open flowers
First flower	Buds with dark pink coloration with few open flowers (<10%)
Early flower	More than 10% but less than 50% of flower buds have opened
Full flower	>50% of flower buds have opened
Post flower	All buds have opened, flowers have become shriveled, color has changed to yellow to brown, and hang down from their pedicels
Early fruiting	Small, green fruits have begun to develop

and southern, respectively. The blocks were located within a garden bed that was surrounded by turf grass and that was next to ornamental trial garden beds to the north and south, a plant production area to the east, and a restored native shoreline to the west. The common garden was mulched with leaf mold, was regularly weeded to maintain bare ground between study plants, and was watered through aerial sprinkler irrigation to maintain normal precipitation for the region. The regular maintenance did not have any noticeable negative effects on the use of the study plants by insect herbivores.

*Plant Phenology, Size, and Fruit Set*

After an initial establishment year in 2015, phenology data were collected over two growing seasons: 2016 (all surviving plants; 109–123 plants/seed source = 350 total) and 2017 (random subset of plants; 30 plants/seed source = 90 total). At least once weekly, phenophase was recorded for each surviving individual in 2016 and thirty randomly tagged individuals per seed source in 2017. Seven stages (phenophases) were used to define individual phenology: vegetative, flower buds, first flower, early flower, full flower, post flower, and early fruiting. These stages are described in Table 2 and, other than the vegetative phase, are illustrated in Figure 1. At the end of the growing season (mid-September), the maximum height of each plant (soil to tallest point) and, for reproductive individuals, the number of follicles (hereafter, fruit) were recorded. Fruits were scored via visual assessment and recorded as viable (full size, rigid, green, not dehiscent) or aborted (immature size, dry and pliant, grey to brown, dehiscent without presence of apparently viable seeds). Milkweeds are known for producing many aborted fruits (Gaertner 1979; Stephenson 1981).

*Floral Visitation*

In year three (2017) pollinator observations were conducted two to three times per week during the flowering period, alternating between morning (10–12am) and afternoon (1–3pm) sessions on warm, sunny days (daily maximum 24–32°C; Chicago Botanic Garden unpublished data). During each session a 2×2m plot in each block was monitored for one 15-minute interval. Plots were randomly selected within each seed source using transects running north to south along the east and west sides of the common garden plot. To ensure visitation was not confounded by time of day, morning and afternoon sessions alternated between east and west transects. Within each observation plot, the length of visitation per plant, the number of plants visited, and the phenophase of both plant(s) and individual umbel(s) visited were recorded for each floral visitor. Observations were conducted in intervals of an average of 15 minutes each for a total of 563 minutes (37 sessions over 10 days) for all seed sources with 136 minutes (9 sessions over 5 days), 219 minutes (14 sessions over 10 days), and 208 minutes (14 sessions over 10 days) for the Minnesota, Illinois, and Missouri blocks, respectively. The Minnesota population had an abbreviated observation window, because its flowering period ended earlier. Average temperature during the course of the study (Apr 2014–Oct 2017, NOAA 2019) largely aligned with climate normals (1970–2000; Fick and Hijmans 2017) for the site (Figure 2). However, the winters of 2016 and 2017 were warmer than average, as were the falls of 2015 and 2016.

*Statistical Analyses*

A coarse estimate of the number of flowers per seed source was calculated as the sum of the number of viable and aborted fruits. Linear models were used to evaluate phenological variation among



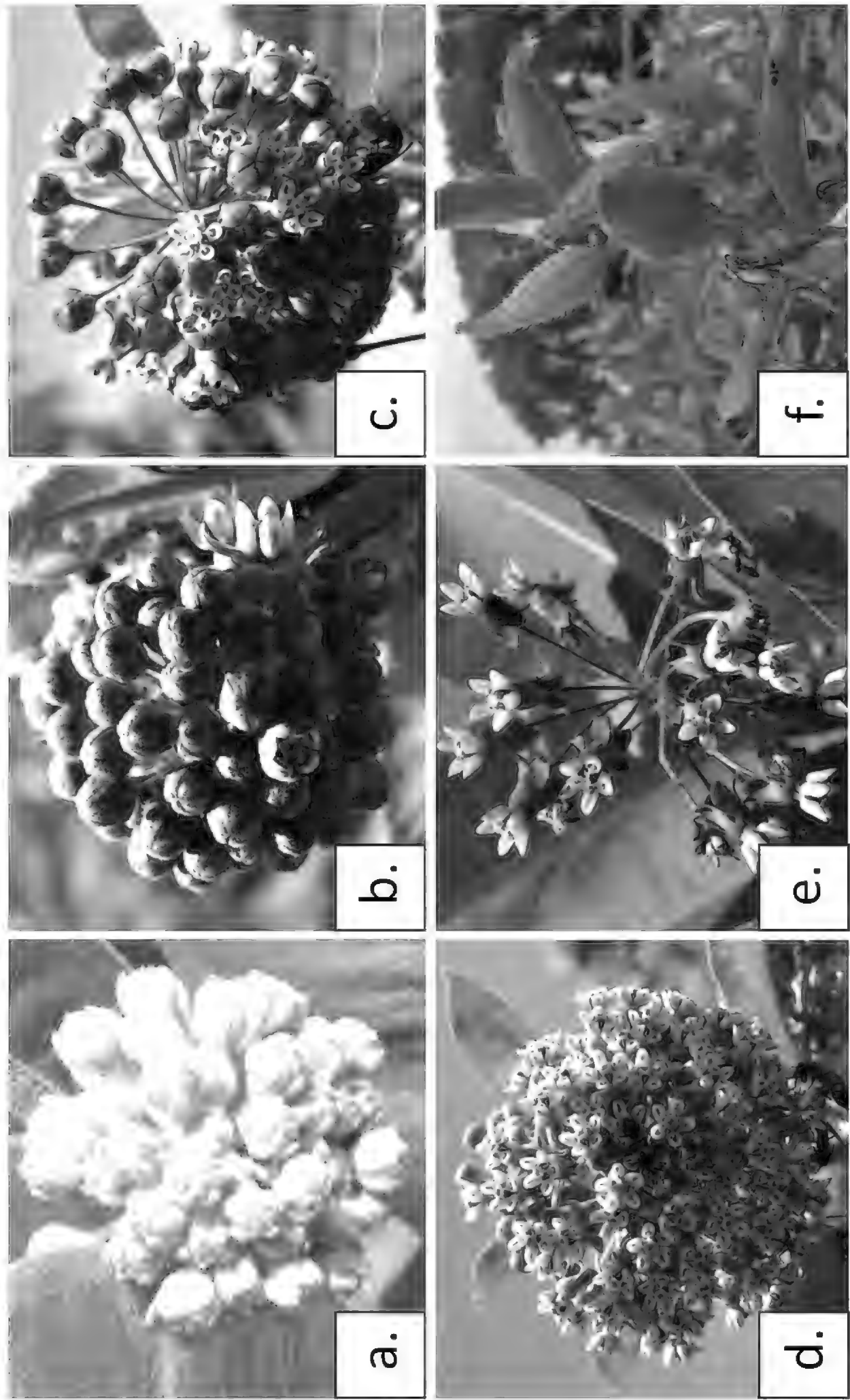


FIGURE 1. Reference photos illustrating six of the seven phenological stages (phenophases) that were used to define individual phenology (the vegetative stage is not pictured): (a) flower buds, (b) first flower, (c) early flower, (d) full flower, (e) post flower, and (f) early fruiting. Descriptions are provided in Table 2.

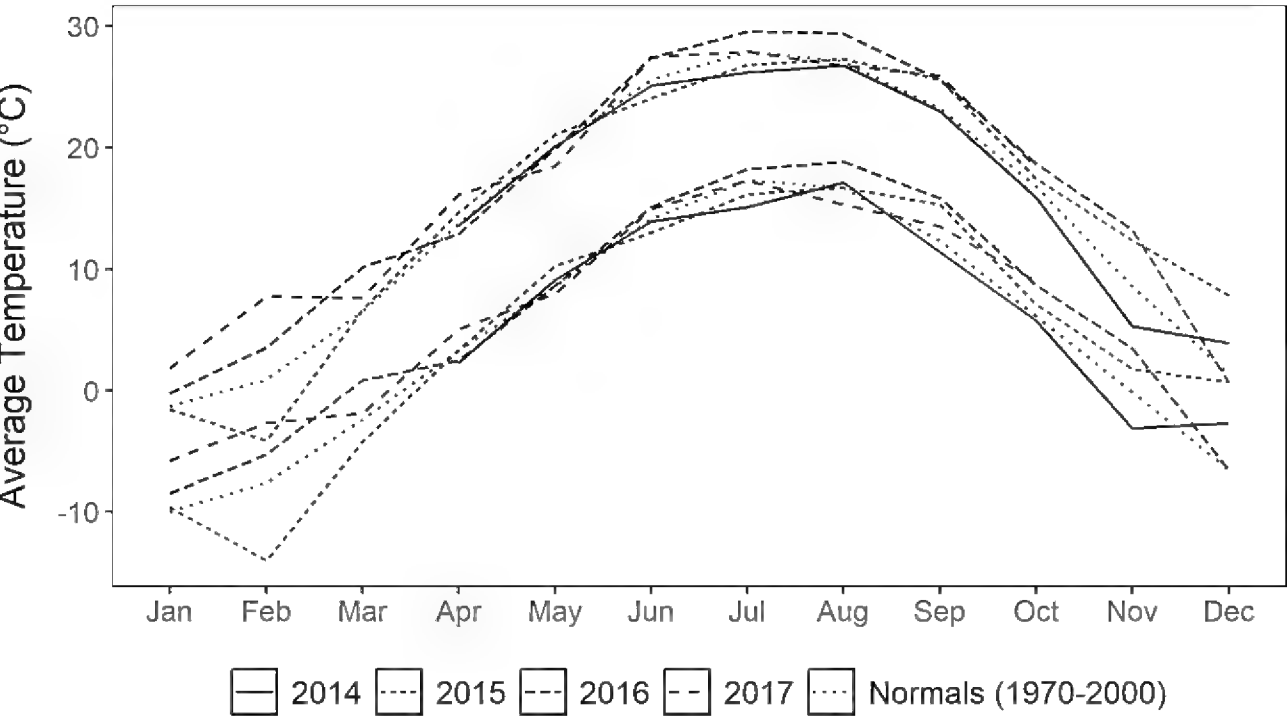


FIGURE 2. Average minimum and maximum monthly temperature for each month during the study period (Apr 2014–Oct 2017), (NOAA 2019) as compared to the monthly temperature normal (min–max; 1970–2000) from WorldClim version 2.1, 30 seconds spatial resolution data (Fick and Hijmans 2017).

seed sources with respect to 1) day of peak flower, and 2) flowering duration. For both phenology models (1 and 2), the date was converted to day of year and due to disparate sample sizes only complete phenology data from 2016 was included. For model 1, the response variable was the average day of peak flower for an individual plant, and the predictor was seed source. For model 2, flowering duration was calculated for individual plants as the number of days from (and including) first flower to the day before post flower was first observed. Variation in floral visitation was tested using generalized linear models (family=quasipoisson) with maximal models including an additive relationship between seed source, observation period, and time of day (morning or afternoon). Variation in visit length (min:sec) by seed source and plant height were evaluated using linear models. Generalized linear models were used to investigate the variation among seed sources in fruit production (number of viable and aborted fruits, family=quasipoisson) and the proportion of viable fruit (family=quasibinomial). All maximal models for fruit set include seed source, year, and the interaction between the two. The best models were selected through backwards elimination, as described in Crawley (2015), and defined as the minimal adequate model to fit the data. Pair-wise significant differences among seed sources were evaluated using the ‘glht’ function for multiple comparisons in parametric models in the package ‘multcomp’ (type= ‘Tukey’) (Hothorn et al. 2017). All analyses were conducted in R: A language and environment for statistical computing (version 4.0.4, 2021-02-15) (R Core Team 2021).

RESULTS

Flowering Phenology and Duration

Averaged across both years, northern plants produced the most flowers (26.6, SD =22.6), 4.5 more than central plants and 14.7 more than southern plants. Flowering phenology was found to vary significantly by seed source for 2016

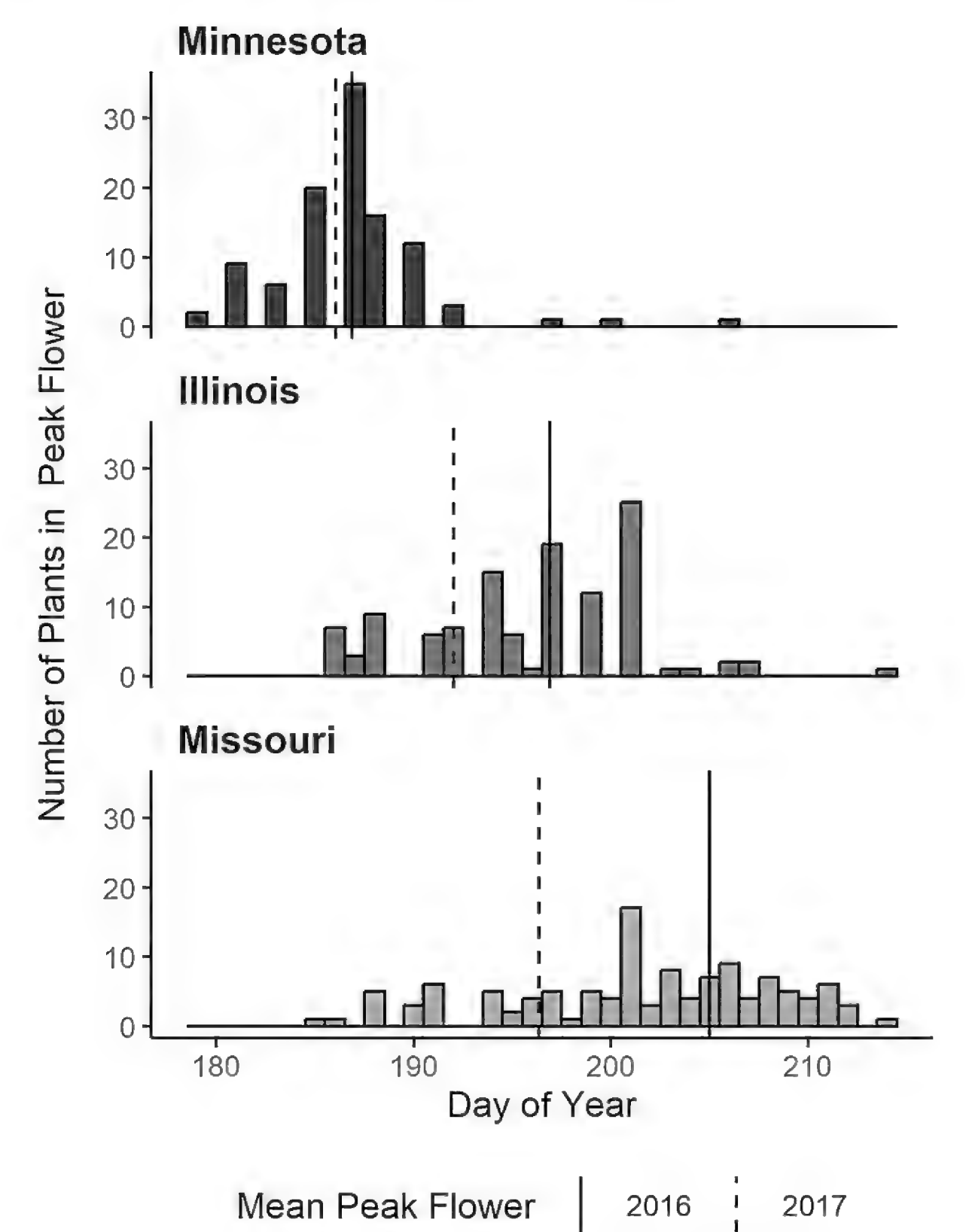


FIGURE 3. Histogram of mean day-of-year of peak flower by seed source in both 2016 and 2017. Vertical lines show the mean day of peak flower for each seed source by year. Seed sources are arranged from north (top, Minnesota) to south (bottom, Missouri).

data ( $P<0.001$ ) (Figure 3). A Tukey’s honest significant difference (HSD) test found all three seed sources varied significantly in mean day of peak flower ( $P\leq0.047$ ), with plants sourced from Minnesota (187,  $SD=4.2$ ) achieving peak flower about 10 days earlier than those from Illinois (197,  $SD=5.4$ ), and Illinois plants about eight days earlier than those from Missouri (205,  $SD=6.1$ ). Flower-

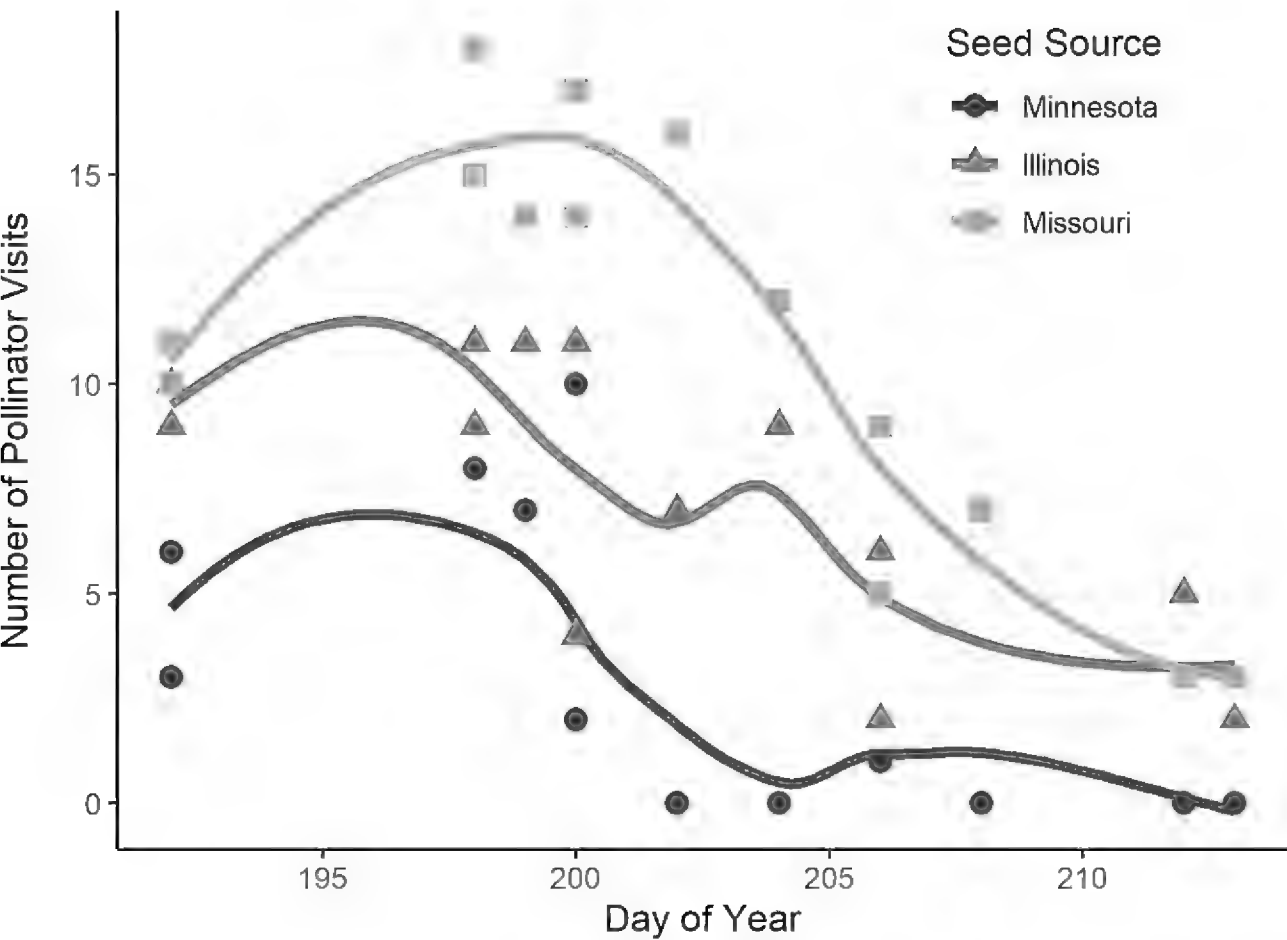


FIGURE 4. The number of floral visits per day for plants from each seed source from observations in 2017. The filled circles, triangles, and squares indicate the number of floral visits per observation period, and the lines visualize smoothed conditional mean (method= ‘loess’) by seed source over time.

ing duration of individual plants did not significantly vary among seed sources (mean=18–21 days). Interannual variation in mean day of peak flower was considerably greater in plants from southern sources (8.63 days) than those from central sources (4.84 days) and northern sources (0.82 days).

Floral Visitation

The number of floral visitors per observation period (15 min) ranged from zero to 18 (Figure 4). The number of visitors varied significantly by seed source and observation date ( $P<0.001$ ), but not by time of day (morning or afternoon), reflecting sequential flowering phenology. On average, plants sourced from Missouri received the greatest number of floral visits per observation period (11,  $SD=5.0$ ), followed by those sourced from Illinois (7.4,  $SD=3.3$ ) and Minnesota (5.3,  $SE=3.1$ ). Length of floral visitation ranged from one second to seven minutes and 21 seconds, with a mean of 54.8 seconds ( $SD=64.9$ ). Analysis of variance found weak evidence ( $P=0.09$ ) for variation in visit length among seed sources, with the longest visits for the Illinois (local) seed source (66.2 s,  $SD=81.5$ ) followed by Minnesota (53.8 s,  $SD=67.4$ ) and Missouri (47.9 s,  $SD=50.4$ ).



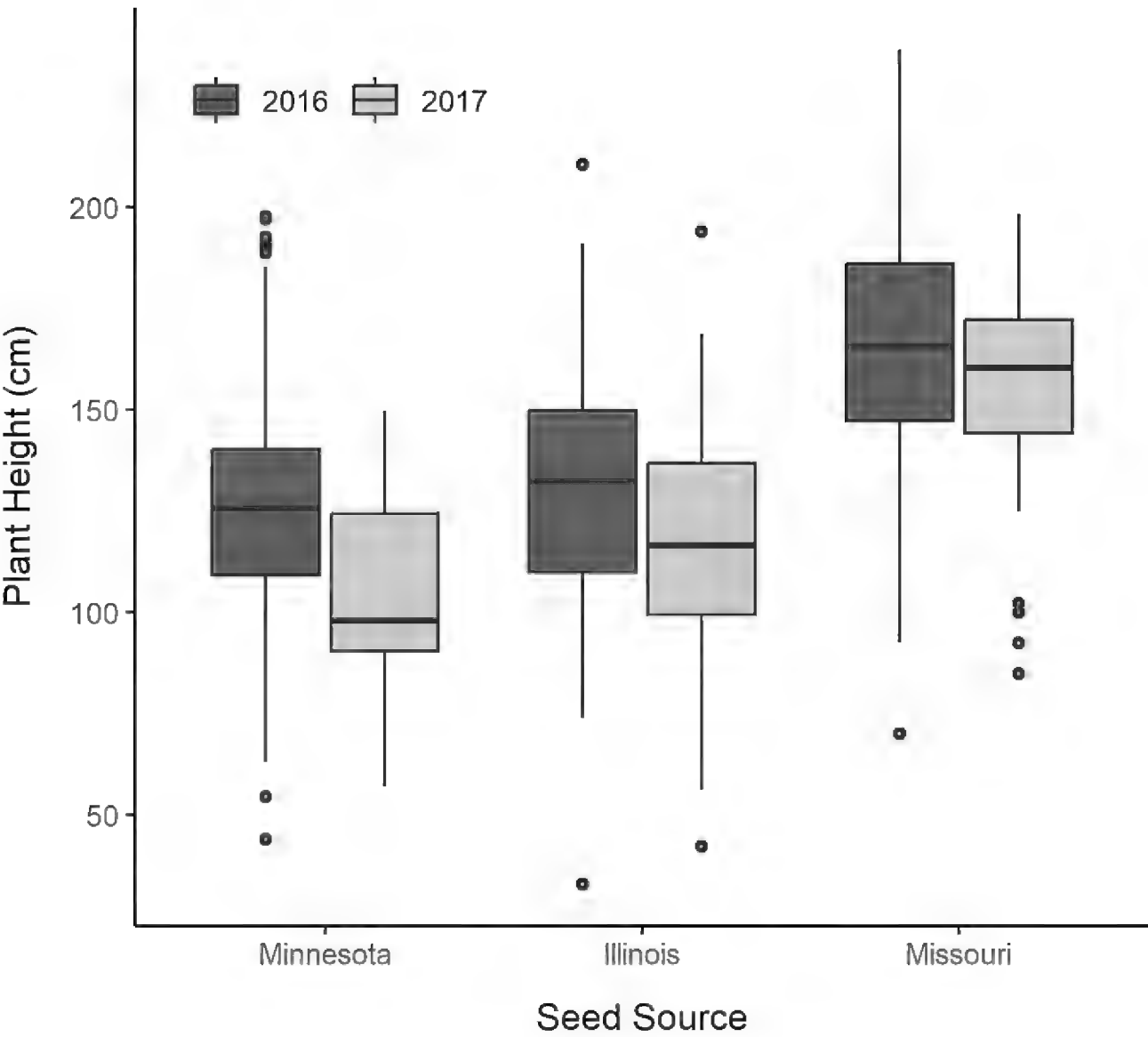


FIGURE 5. Boxplot of plant height by seed source and year. The box shows the second and third quartiles, with a line at the median. The length of the box is the interquartile range (IQR). The whiskers extend to the minimum ( $Q1 - 1.5 \times IQR$ ) and maximum ( $Q3 + 1.5 \times IQR$ ), and the dots indicate outliers. Height was measured at the end of the growing season (mid-September). Seed sources are arranged on the x-axis from north (left, Minnesota) to south (right, Missouri). Box color denotes the year (2016 = dark grey, 2017 = light grey).

Plant Height

The best fit linear model found that plant height varied significantly among seed source and year, with each predictor having an additive effect ( $P < 0.001$ ) (Figure 5). In both years the late-flowering plants from the Missouri seed source were the tallest of the three sources (mean=161, SD=31.0 cm), followed by those from the mid-flowering Illinois source (128, SD=30.3 cm), with the early-flowering plants from the Minnesota source exhibiting the shortest plant height (122, SD=31.1 cm). Tukey’s HSD test found the height of Missouri sourced plants was significantly greater than those from both Illinois and Minnesota sources ( $P < 0.001$ ), but plant height did not significantly differ between plants from Illinois and Minnesota ( $P = 0.278$ ). Plant height was significantly greater in 2016 than in 2017 ( $P < 0.001$ ). On average, plants sourced from Missouri were 10 cm

taller, plants sourced from Illinois were 14 cm taller, and plants sourced from Minnesota were 26 cm taller in 2016 than in 2017.

Fruit Set and Abortion

The minimal adequate model for viable fruit set was an additive generalized linear model including seed source and year (2016, 2017). Overall, the number of viable fruits varied among seed sources with plants from the Illinois source (mean=11.6, SD=12.2) producing significantly more than those from either Missouri (8.59, SD=7.87) or Minnesota (6.81, SD=7.27;  $P\leq0.03$ ) when summed across both years. However, the elevated fruit count of plants sourced from Illinois was overwhelmingly influenced by the first data collection year (2016; 12.7, SD=13.1). The minimal adequate model for fruit abortion was the maximal model, which includes an interaction term between seed source and year. The number of aborted fruits varied significantly among seed sources, with the great-

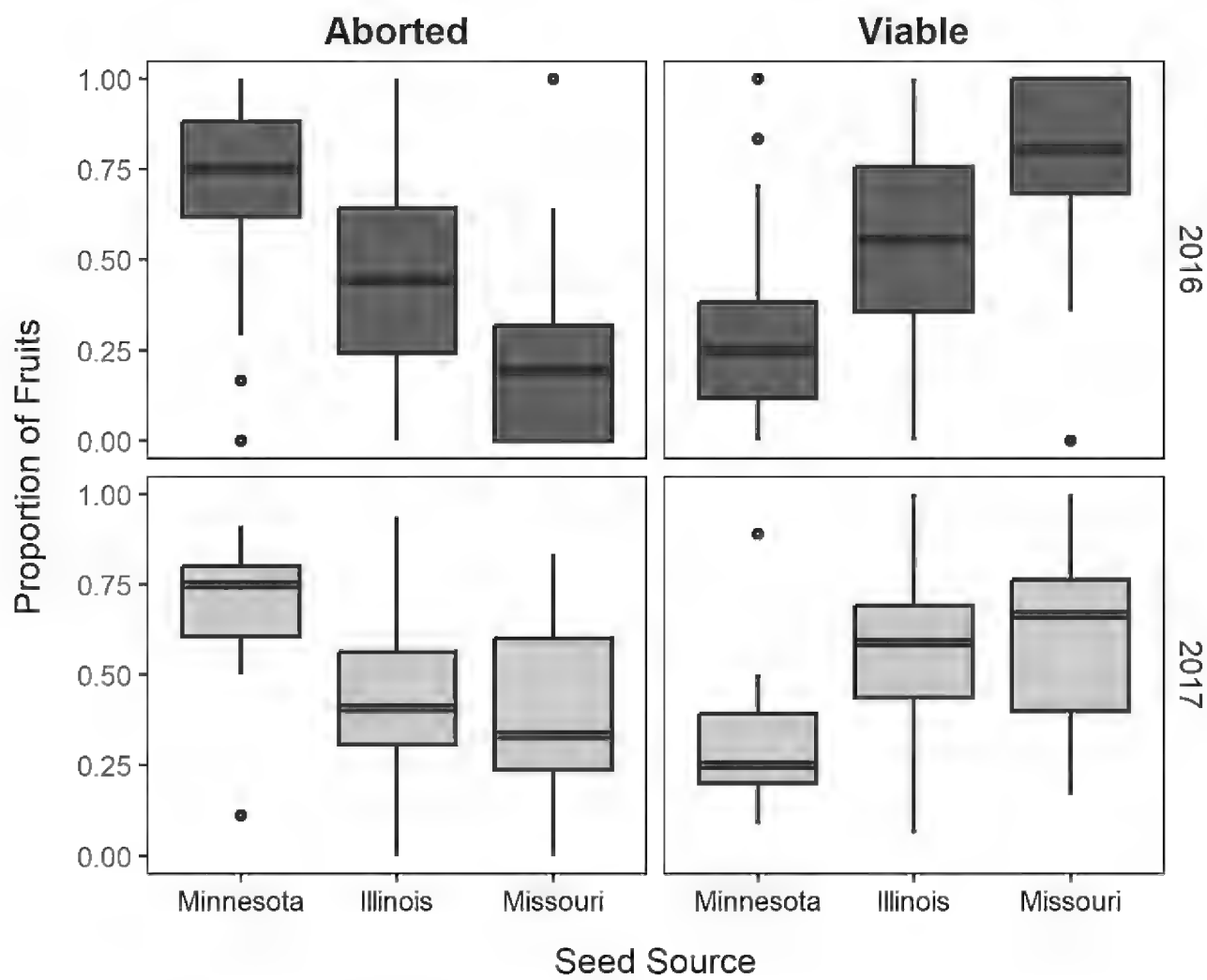


FIGURE 6. Boxplot of fruit set (proportion aborted and viable) by seed source and year. The box shows the second and third quartiles, with a line at the median. The length of the box is the interquartile range (IQR). The whiskers extend to the minimum ( $Q1 - 1.5 \times IQR$ ) and maximum ( $Q3 + 1.5 \times IQR$ ), and the dots indicate outliers. Box color denotes the year (2016 = dark grey, 2017 = light grey). Proportion of aborted fruits (left column) varied by seed source and declined with the latitude of the seed source origin, while viable fruit production demonstrated the opposite pattern in variation by latitude (right column). This trend persisted over two growing seasons (2016 and 2017).

est number observed for Minnesota plants (mean=19.8, SD=18.6) followed by Illinois (10.5, SD=11.9) and Missouri (3.32, SD=4.64;  $P < 0.001$ ). The minimal adequate model for the proportion of viable fruit retained a singular factor: population. All populations differed significantly from each other in the proportion of viable fruit ( $P < 0.001$ ), with Missouri having the highest proportion of viable fruit (0.73, SD=0.23), followed by Illinois (0.55, SD=0.25), and Minnesota (0.28, SD=0.20) (Figure 6).

## DISCUSSION

Common garden performance over multiple years demonstrated significant variation among common milkweed seed sources in flowering phenology, floral visitation, height, and reproduction. In step with latitude and climate of the mid-western United States, northern plants from cooler climates with shorter growing seasons were shorter and flowered earlier than southern plants. Later flowering phenology was associated with increased floral visitation and may have driven the observed variation in fruit set. Specifically, southern plants flowered later and produced more viable fruits and fewer aborted fruits than northern plants, both in total count and relative proportion. These patterns appear to be the result of heritable genetic variation and not maternal effects, as they persisted over three years, including two resprout generations of the herbaceous, perennial plant. However, transgenerational phenotypic plasticity cannot be excluded as a contributor of the observed variation, as the maternal plants grew in disparate geographic and climatic environments (Herman and Sultan 2011).

Interestingly, persistent geographic variation is inconsistent with a recent study on range-wide variation in vegetative common milkweed traits and their effect on monarch larvae (DeLaMater et al. 2021). Biogeographic clines were found for all but three of 13 traits considered, but clines did not persist in a greenhouse common garden environment over 12 months and two resprout generations. The DeLaMater et al. (2021) study did not consider reproductive traits, but their field measurements also found northern plants to be shorter, as was observed in the outdoor common garden study presented here. An independent effort, the Milkweed Adaptation Research and Education Network (MAREN 2024) was founded in 2015 at St. Olaf College in Minnesota to investigate local adaptation in common milkweed. Their recent paper found evidence of a latitudinal cline in germination, with northern sources germinating faster and to a higher proportion (Mohl et al. 2023). Other MAREN studies have investigated plant-monarch interactions, finding a positive correlation between leaf number, source latitude (Rice et al. 2021), and presence of monarch eggs (Msuya et al. 2021). When taken together with the results from this study, potential divergent advantages for herbivores and nectarivores appear, as southern sources may provide floral visitors with a longer flowering period during which to nectar, but northern sources may produce more leaves, making them more attractive for monarch oviposition. These potential tradeoffs are especially impactful given that common milkweed supports not only monarchs but 112 unique insect

species, including nine specialist herbivores (Wilhelm and Rericha 2017; Miles et al. 2022). Additional studies are still needed to elucidate the relative genetic and environmental contributions to clines in vegetative and reproductive traits in this widespread and ecologically significant species.

Previous work on common milkweed found the number of mature pods per stem is positively correlated with the number of inflorescences (umbels) per stem and the number of flowers per inflorescence (Willson and Rathcke 1974; Willson and Price 1977). This may be explained in part by a demonstrated positive correlation between floral display size and length of floral visits, which was found to positively impact female plant fitness in this species (La Rosa and Conner 2017). However, a coarse estimate of the relative number of flowers produced in this study found northern plants produced the most flowers on average, despite producing the fewest and lowest proportion of viable fruits of the three seed sources. It is important to note this estimate does not consider the number of umbels per stem or the size of umbels (number of flowers per inflorescence), which is known to impact pollinator visitation and viable fruit set (Willson and Price 1977).

Variation in flowering phenology within populations is known to impact fitness in this genus, with fruit set for late-flowering plants about twice that of early-flowering plants (Kephart 1987). Greater variation was observed among seed sources than within seed sources, difference in fruit set among seed sources were very similar to this finding, with about a twofold increase in viable fruit set between the earliest flowering seed source (Minnesota) and the middle flowering seed source (Illinois), and a threefold increase between the earliest flowering seed source and the latest flowering seed source (Missouri). Interestingly, the latitudinal cline in flowering phenology observed was consistent with a recent study of three perennial forb species in Minnesota where opposite impacts for fitness were found (Rushing et al. 2021). In addition to impacting reproductive fitness, variation in flowering phenology has implications for gene flow among individuals and populations as a result of greater or less flowering synchrony within and between populations (Rivest et al. 2021). Increased variation in intraspecific flowering phenology may benefit pollinators through greater temporal diversity in nectar resources, particularly in species-poor communities not benefiting from interspecific variation. However, decreased flowering synchrony can reduce cross-pollination, with implications for reproductive success, maintenance of genetic diversity, and evolutionary potential (Franklin and Frankham 1998; Richardson and Wagenius 2021).

Appropriate sourcing of plant material for ecological restoration and/or habitat creation is vital for the successful establishment and persistence of the targeted plant community, as well as ecological function (Gallagher and Wagenius 2015; Erickson and Halford 2020; Kettenring and Tarsa 2020). In the past decade awareness of the plight of the monarch butterfly, specifically the imperiled annual migration of the eastern North American population, has spurred swift and significant investment in the creation of monarch habitat throughout the summer breeding range (Lewandowski and Oberhauser 2016; Thogmartin et al. 2017a). Plant species composition of constructed or restored monarch habitat can vary but must include one or more species of milkweed (*Asclepias* spp.), the

obligate larval host of the monarch butterfly, which also serve as important nectar plants for monarchs and other pollinators (Southwick 1983; Tillman and Carpenter 2014; Wilson 2021). It is also recommended plantings include a diversity of nectar-producing plants with bloom times spanning the entire growing season and migration period, from spring through fall (Havens and Vitt 2016). The findings of this study demonstrate the impact of seed sourcing on intraspecific variation in plant traits directly related to plant reproduction and pollinator resources, with southern sources flowering later and producing more viable fruits than northern sources. Interestingly, results indicate a mix of seed sources can increase the blooming period of a species in a single location by two to six times, or 30–50 days. Given the substantial clonal spread of common milkweed, as well as the numerous seeds contained in a single fruit, experimenting with increased variation in flowering phenology through mixing of seed sources may be a net positive for pollinators without any significant loss to species recruitment (Betz and Lamp 1992; He and Agrawal 2020).

In addition to seed sourcing, these data must also be interpreted in the context of climate change. An analysis of flowering phenology across the native range of common milkweed found higher temperatures were correlated with symmetrical phenology shifts earlier (Howard 2018). Common milkweed plants moved to a cooler climate (e.g., seed from Missouri moved to the common garden in Illinois) fared well, but plants moved to a warmer climate (e.g., seed from Minnesota moved to the common garden in Illinois) demonstrated decreased reproduction 20–40% below that of plants sourced locally or from further south. These results suggest that reproductive capacity could decrease under climate change, potentially hampering population growth and the capacity to colonize new sites. Common milkweed produces wind-dispersed seeds, and plant height is expected to impact seed dispersal distance, with dispersal distance increasing with height of release (Morse and Schmitt 1985). Therefore, the impact of climate change on phenology and plant height at point of seed dispersal has implications for the number of seeds produced and their dispersal ability. The results indicate decreased performance under climate change, but simultaneously provide a potential mitigation strategy: the introduction of southern genotypes. To keep pace with rapid climate change, land management practitioners could introduce seeds from southern sources to naturally occurring or restored populations. Climate-informed sourcing is actively under investigation for a wide range of plant taxa (e.g., Jochems et al. 2022; St. Clair et al. 2022; Woolridge et al. 2023) with a segment of the restoration community trending towards the recommendation of mixing sources within a region (e.g., Bucharova et al. 2019; Hancock et al. 2023; Nolan et al. 2023). Given sufficient overlap in flowering times, interbreeding between local and non-local sources could introduce adaptive phenological traits and expedite adaptation to changing climates (Aitken and Whitlock 2013). However, studies of additional common milkweed populations across multiple field sites are necessary to determine the extent of phenological variation and the potential value of and risks associated with assisted gene flow to maintain population fitness under climate change.

In summary, wild-collected seed from three populations of common milkweed located across a 750 km latitudinal gradient in the midwestern United



States demonstrated persistent phenological and phenotypic differences in a centrally located common garden over multiple growing seasons. Plants from northern sources flowered earlier, were shorter at maturity, and demonstrated considerably less interannual variation in phenology than those from southern sources. Plants from southern sources, which flowered later, received greater floral visitation, and produced more viable fruits than those from northern sources. These results suggest that plants from southern sources may perform better than those from local or northern sources under restoration settings. In addition, the results suggest populations of common milkweed may demonstrate decreased fruit production under climate change, with implications for population persistence and colonization of new sites. However, assisted gene flow through the introduction of seed from southern populations to higher latitudes could contribute novel adaptive phenological traits and expedite adaptation to changing climates. Additionally, these results suggest mixing of seed sources can greatly expand flowering windows in restored or constructed habitats with implications for pollinator conservation. Relatedly, mid-season mowing of milkweed has been shown to be a successful management strategy for supporting monarch reproduction because it serves as a phenological reset and adult monarchs prefer to oviposit on regenerating milkweed stems free from enemies (Fischer et al. 2015; Haan and Landis 2019; Knight et al. 2019). We encourage future studies to investigate how mixed-source milkweed restorations may provide valuable phenological variation without the need for mowing, which does pose risks for the invertebrate community.

#### AUTHOR CONTRIBUTIONS

Conceptualization, K.H., and J.F.; seed collection, J.F. and K.H.; methodology, J.F. and K.H.; data collection, I.V. and J.F.; formal analysis, J.F.; data curation, J.F. and I.V.; writing—original draft preparation, J.F., I.V., and K.H.; writing—review and editing, J.F., I.V., and K.H.; visualization, J.F. and I.V.; supervision, K.H. and J.F.; All authors have read and agreed to the published version of the manuscript.

#### ACKNOWLEDGMENTS

We would like to thank Ginger Allington, formerly of the Missouri Botanical Garden, and Ricky Garza, of the Minnesota Landscape Arboretum, for seed collection; the Chicago Botanic Garden Horticulture staff for propagation and garden maintenance, especially Jamie Berlin; Lake Forest College BIO 384 Plant Biology students for reproductive trait measurements (2015–2018); and interns Tia Chung-Swanson and Rachel Krebs for field data collection (2016). This work was supported in part by the Chicago Botanic Garden's College First and REU Site Programs (under the 2017 NSF grant DBI-1461007). Lastly, we are grateful to the three anonymous reviewers who provided helpful comments on earlier drafts of this manuscript.

#### LITERATURE CITED

- Aitken, S. N., and M. C. Whitlock. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44: 367–388.
- Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Mitchell-Olds. (2012). Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B* 279: 3843–3852.

- Betz, R. F., and H. F. Lamp. (1992). Flower, pod, and seed production in eighteen species of milkweeds (*Asclepias*). Pp. 25–30 in Proceedings of the twelfth North American prairie conference: Recapturing a vanishing heritage, D. D. Smith and C. Jacobs, editors. University of Northern Iowa, Cedar Falls, Iowa.
- Breed, M. F., P. A. Harrison, A. Bischoff, P. Durruty, N. J. C. Gellie, E. K. Gonzales, K. Havens, et al. (2018). Priority actions to improve provenance decision-making. *BioScience* 68: 510–516.
- Broadhurst, L. M., A. Lowe, D. J. Coates, S. A. Cunningham, M. McDonald, P. A. Vesk, and C. Yates. (2008). Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1: 587–597.
- Brower, L. P., O. R. Taylor, E. H. Williams, D. A. Slayback, R. R. Zubieta, and M. I. Ramírez. (2012). Decline of monarch butterflies overwintering in Mexico: Is the migratory phenomenon at risk? *Insect Conservation and Diversity* 5: 95–100.
- Bucharova, A., M. Frenzel, K. Mody, M. Parepa, W. Durka, and O. Bossdorf. (2016). Plant ecotype affects interacting organisms across multiple trophic levels. *Basic and Applied Ecology* 17: 688–695.
- Bucharova, A., O. Bossdorf, N. Hölzel, J. Kollman, R. Prasse, and W. Durka (2019). Mix and match: Regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics* 20: 7–17.
- Bucharova, A., C. Lampei, M. Conrady, E. May, J. Matheja, M. Meyer, and D. Ott. (2021). Plant provenance affects pollinator network: Implications for ecological restoration. *Journal of Applied Ecology* 59: 373–383.
- CBD. (2024). Convention on Biological Diversity. Decision adopted by the Conference of the Parties to the Convention on Biological Diversity on 1 November 2024. Available at [www.cbd.int/doc/decisions/cop-16/cop-16-dec-20-en.pdf](http://www.cbd.int/doc/decisions/cop-16/cop-16-dec-20-en.pdf). (Accessed January 18, 2025)
- Crawley, M. J. (2015). *Statistics: An introduction using R*, Second Edition. Wiley, Imperial College London, UK.
- DeLaMater, D. S., J. J. Couture, J. R. Puzey, and H. J. Dalglish. (2021). Range-wide variations in common milkweed traits and their effect on monarch larvae. *American Journal of Botany* 108: 388–401.
- Durant, J. M., D. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N. C. Stenseth. (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8: 952–958.
- Erickson, V. J., and A. Halford. (2020). Seed planning, sourcing, and procurement. *Restoration Ecology* 28: S219–S227.
- Fick, S. E., and R. J. Hijmans. (2017). WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315. Available at <https://www.worldclim.org/data/worldclim21.html>. (Accessed January 20, 2025)
- Fischer, S. J., E. H. Williams, L. P. Brower, and P. A. Palmiotto. (2015). Enhancing monarch butterfly reproduction by mowing fields of common milkweed. *American Midland Naturalist* 173: 229–240.
- Flockhart, D. T. T., J.-B. Pichancourt, D. R. Norris, and T. G. Martin. (2014). Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology* 84: 155–165.
- Forrest, J. R. K. (2014). Plant–pollinator interactions and phenological change: What can we learn about climate impacts from experiments and observations? *Oikos* 124: 4–13.
- Franklin, I. R., and R. Frankham. (1998). How large must populations be to retain evolutionary potential? *Animal Conservation* 1: 69–70.
- Gaertner, E. A. (1979). The history and use of milkweed (*Asclepias syriaca* L.). *Economic Botany* 33: 119–123.
- Gallagher, M. K., and S. Wagenius. (2015). Seed source impacts germination and early establishment of dominant grasses in prairie restorations. *Journal of Applied Ecology* 53: 251–263.
- Gehring, C. A., C. M. Sthultz, L. Flores-Rentería, A. V. Whipple, and T. G. Whitham. (2017). Tree genetics defines fungal partner communities that may confer drought tolerance. *Proceedings of the National Academy of Science of the United States of America* 114: 11169–11174.
- Genes, L., and R. Dirzo. (2022). Restoration of plant-animal interactions in terrestrial ecosystems. *Biological Conservation* 265: 109393.
- Gosney, B., J. O'Reilly-Wapstra, L. Forster, C. Whiteley, and B. Potts. (2017). The extended com-

- munity-level effects of genetic variation in foliar wax chemistry in the forest tree eucalyptus globulus. *Journal of Chemical Ecology* 43: 532–542.
- Haan, N. L. and D. A. Landis. (2019). Grassland disturbance increases monarch butterfly oviposition and decreases arthropod predator abundance. *Biological Conservation* 233: 185–192.
- Hancock, N. M., F. Encinas-Viso, and L. M. Broadhurst. (2023). A documented paradigm shift in seed sourcing: attitudinal changes to using local native seed for ecological restoration. *Restoration Ecology* 31: e13845.
- Hartzler, R. G., and D. D. Buhler. (2000). Occurrence of common milkweed (*Asclepias syriaca*) in cropland and adjacent areas. *Crop Protection* 19: 363–366.
- Havens, K., and P. Vitt. (2016). The importance of phenological diversity in seed mixes for pollinator restoration. *Natural Areas Journal* 36: 531–537.
- Havens, K., P. Vitt, S. Still, A. T. Kramer, J. B. Fant, and K. Schatz. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal* 35: 122–133.
- He, E., and A. A. Agrawal. (2020). Clonal versus non-clonal milkweeds (*Asclepias* spp.) respond differently to stem damage, affecting oviposition by monarch butterflies. *PeerJ* 8: e10296.
- Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist* 173: 579–588.
- Herman, J. J., and S. E. Sultan. (2011). Adaptive transgenerational plasticity in plants: Case studies, mechanisms, and implications for natural populations. *Frontiers in Plant Sciences* 2: 102.
- Hobbs, R. J., and V. A. Cramer. (2008). Restoration ecology: Interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annual Review of Environment and Resources* 33: 39–61.
- Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheib. (2017). Package “multcomp” - Simultaneous inference in general parametric models. Available at <https://doi.org/https://cran.r-project.org/web/packages/multcomp/multcomp.pdf>. (Accessed July 18, 2024).
- Howard, A. F. (2018). *Asclepias syriaca* (common milkweed) flowering date shift in response to climate change. *Scientific Reports* 8: 17802.
- IUCN. (2020). The Bonn Challenge. Available at <https://www.bonnchallenge.org/>. (Accessed January 18, 2025).
- Jochems, L. W., J. A. Lau, L. A. Brudvig, and E. Grman. 2022. Do southern seed or soil microbes mitigate the effects of warming on establishing prairie plant communities? *Ecological Applications* 32: e02487.
- Johnson, G., F. C. Sorensen, J. B. S. Clair, and R. C. Cronn. (2004). Pacific Northwest forest tree seed zones. *Native Plants Journal* 5: 131–140.
- Kettenring, K. M., and E. E. Tarsa. (2020). Need to seed? Ecological, genetic, and evolutionary keys to seed-based wetland restoration. *Frontiers in Environmental Science* 8: 109.
- Kephart, S. R. (1987). Phenological variation in flowering and fruiting of *Asclepias*. *American Midland Naturalist* 118: 64–76.
- Knight, S. M., D. R. Norris, R. Derbyshire, and D. T. T. Flockhart. (2019). Strategic mowing of roadside milkweeds increases monarch butterfly oviposition. *Global Ecology and Conservation* 19: e00678.
- Kramer, A. T., and K. Havens. (2009). Plant conservation genetics in a changing world. *Trends in Plant Science* 14: 599–607.
- La Rosa, R. J., and J. K. Conner. (2017). Floral function: Effects of traits on pollinators, male and female pollination success, and female fitness across three species of milkweeds (*Asclepias*). *American Journal of Botany* 104(1): 150–160.
- Leimu, R., and M. Fischer. (2008). A meta-analysis of local adaptation in plants. *PLoS One* 3: e4010.
- Lewandowski, E. J., and K. S. Oberhauser. (2016). Contributions of citizen scientists and habitat volunteers to monarch butterfly conservation. *Human Dimensions of Wildlife* 22: 55–70.
- Malcolm, S. B. (1994). Milkweeds, monarch butterflies and the ecological significance of cardenolides. *Chemoecology* 5: 101–117.
- MAREN. (2024). Milkweed adaptation research and education network. Available at <https://pages.stolaf.edu/milkweed/> (Accessed January 22, 2025)
- McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. (2005). “How Local Is Local?”—A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13: 432–440.

- Memmot, J., P. G. Craze, N. M. Waser, and M. V. Price. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters* 10: 710–717.
- Midwest Association of Fish and Wildlife Agencies. (2018). Mid-America monarch conservation strategy, 2018–2038, Version 1.0. Available at [https://www.mafwa.org/wp-content/uploads/2018/07/MAMCS\\_June2018\\_Final.pdf](https://www.mafwa.org/wp-content/uploads/2018/07/MAMCS_June2018_Final.pdf). (Accessed July 18, 2024).
- Miles, L. S., D. Murray-Stoker, V. J. Nhan, and M. T. J. Johnson. (2022). Effects of urbanization on specialist insect communities of milkweed are mediated by spatial and temporal variation. *Ecosphere* 13: e4222.
- Mohl, E. K., A. C. McCall, M. Wood, L. Sherman, M. V. Reid, P. A. Saunders, S. E. Scanga, et al. (2023). Common milkweed seeds exhibit latitudinal clines more consistent with adaptation to growing season length than temperature. *Restoration Ecology* 31: e13878.
- Morse, D. H., and J. Schmitt. (1985). Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. *Oecologia* 67: 372–379.
- Mortlock, B. W. (2000). Local seed for revegetation. *Ecological Management & Restoration* 1: 93–101.
- Msuya, K., L. Sherman, S. Ronneberg, S. Dlamini, and E. Mohl. (2021). Colonization trends in common milkweed, *Asclepias syriaca*, in central Minnesota. CURI Program Fall Showcase, St. Olaf College. Available at: <https://pages.stolaf.edu/milkweed/wp-content/uploads/sites/1333/2022/03/MSUYA.SHERMAN.RONNBERG.DLAMINI.MOHL-CURI2021-POSTER.pdf>. (Accessed January 22, 2025).
- NOAA. (2019). National Oceanic and Atmospheric Administration, National Centers for Environmental Information, Climate Data Online. Station: Chicago Botanic Garden, IL US (GHCND:USC00111497). Available at: <https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00111497/detail>. (Accessed January 20, 2025).
- Nolan, M.P., J. C. Luong, J. M. Valliere, S. J. Mazer, and C. M. D’Antonio. (2023). Rethinking local seed sourcing for the restoration of a foundational grass species in California. *Restoration Ecology* 31: e13992.
- Peralta, G., D. P. Vázquez, N. P. Chacoff, S. B. Lomáscolo, G. L. W. Perry, and J. M. Tylianakis. (2020). Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. *Ecology Letters* 23: 1107–1116.
- Piao, S., Q. Liu, A. Chen, I. A. Janssens, Y. Fu, J. Dai, L. Liu, et al. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology* 25: 1922–1940.
- Pleasants, J. (2017). Milkweed restoration in the Midwest for monarch butterfly recovery: Estimates of milkweeds lost, milkweeds remaining and milkweeds that must be added to increase the monarch population. *Insect Conservation and Diversity* 10: 42–53.
- Prober, S. M., M. Byrne, E. H. McLean, D. A. Steane, B. M. Potts, R. E. Vaillancourt, and W. D. Stock. (2015). Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution* 3: 65.
- R Core Team. (2021). R: A language and environment for statistical computing. Available at <https://www.R-project.org/>. (Accessed July 18, 2024).
- Rice, S., C. Wilkens, M. Wood, and E. Mohl. (2021). Evidence of geographic local adaptation in fitness and growth traits of *Asclepias syriaca*. CURI Program Fall Showcase, St. Olaf College. Available at: <https://pages.stolaf.edu/milkweed/wp-content/uploads/sites/1333/2022/03/RICE-WILKENS-WOOD-MOHL-CURI-2021-Poster-1-compressed.pdf>. (Accessed January 22, 2025).
- Richardson, L. K., and S. Wagenius. (2021). Fire influences reproductive outcomes by modifying flowering phenology and mate-availability. *New Phytologist* 233: 2083–2093.
- Rivest, S., G. Lajoie, D. A. Watts, and M. Velland. (2021). Earlier spring reduces potential for gene flow via reduced flowering synchrony across an elevational gradient. *American Journal of Botany* 108: 538–545.
- Rushing, N. S., S. A. Flint, and R. G. Shaw. (2021). Latitude of seed source impacts flowering phenology and fitness in translocated plant populations. *Restoration Ecology* 29: e13464.
- Seiber, J. N., L. P. Brower, S. M. Lee, M. M. McChesney, H. T. A. Cheung, C. J. Nelson, and T. R. Watson. (1986). Cardenolide connection between overwintering monarch butterflies from Mexico and their larval food plant, *Asclepias syriaca*. *Journal of Chemical Ecology* 12: 1157–1170.
- Semmens, B. X., D. J. Semmens, W. E. Thogmartin, R. Wiederholt, L. López-Hoffman, J. E. Diffendorfer, J. M. Pleasants, et al. (2016). Quasi-extinction risk and population targets for the Eastern, migratory population of monarch butterflies (*Danaus plexippus*). *Scientific Reports* 6: 1–7.

- Society for Ecological Restoration International Science & Policy Working Group. (2004). The SER International Primer on Ecological Restoration. Available at [https://www.ctahr.hawaii.edu/lit-tonc/PDFs/682\\_SERPrimer.pdf](https://www.ctahr.hawaii.edu/lit-tonc/PDFs/682_SERPrimer.pdf). (Accessed July 18, 2024).
- Southwick, E. E. (1983). Nectar biology and nectar feeders of common milkweed, *Asclepias syriaca* L. *Journal of the Torrey Botanical Society* 110: 324–334.
- St.Clair, J. B., B. A. Richardson, N. Stevenson-Molnar, G. T. Howe, A. D. Bower, V. J. Erickson, B. Ward, et al. (2022). Seedlot selection tool and climate-smart restoration tool: Web-based tools for sourcing seed adapted to future climates. *Ecosphere* 13: e4089.
- Stephenson, A. G. (1981). Flower and fruit abortion: Proximate causes and ultimate functions. *Annual Review of Ecology, Evolution, and Systematics* 12: 253–279.
- Thogmartin, W. E., L. López-Hoffman, J. Rohweder, J. Diffendorfer, R. Drum, D. Semmens, S. Black, et al. (2017a). Restoring monarch butterfly habitat in the midwestern US: “All hands on deck.” *Environmental Research Letters* 12: 074005.
- Thogmartin, W. E., R. Wiederholt, K. Oberhauser, R. G. Drum, J. E. Diffendorfer, S. Altizer, O. R. Taylor, et al. (2017b). Monarch butterfly population decline in North America: Identifying the threatening processes. *Royal Society Open Science* 4: 170760.
- Tillman, P. G., and J. E. Carpenter. (2014). Milkweed (Gentianales: Apocynaceae): A farmscape resource for increasing parasitism of stink bugs (Hemiptera: Pentatomidae) and providing nectar to insect pollinators and monarch butterflies. *Environmental Entomology* 43: 370–376.
- Trudeau, J., B. Obama, and E. Peña. (2016). Leaders’ statement on a North American climate, clean energy, and environment partnership. Available at <https://www.pm.gc.ca/en/news/statements/2016/06/29/leaders-statement-north-american-climate-clean-energy-and-environment>. (Accessed July 18, 2024).
- UN. (2015). Transforming our world: The 2030 agenda for sustainable development. Available at <https://sdgs.un.org/publications/transforming-our-world-2030-agenda-sustainable-development-17981>. (Accessed January 18, 2025).
- UNEP. (2024). United Nations Decade on Ecosystem Restoration 2021–2030. Available at <https://www.decadeonrestoration.org/>. (Accessed January 22, 2025).
- USDOI. (2024). U.S. Department of the Interior. America the beautiful. Available at <https://www.doi.gov/priorities/america-the-beautiful>. (Accessed January 19, 2025).
- Wilhelm, G., and L. Rericha. (2017). Flora of the Chicago region: A floristic and ecological synthesis. Indiana Academy of Science, Indianapolis.
- Willson, M. F., and P. W. Price. (1977). The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495.
- Willson, M. F. and B. J. Rathcke. (1974). Adaptive design of the floral display in *Asclepias syriaca* L. *American Midland Naturalist* 92: 47.
- Wilson, J. S. (2021). What North American bees are associated with milkweed (*Asclepias*) flowers? *Western North American Naturalist* 81: 171–180.
- Woolridge, C. B., J. B. Fant, A. I. Flores, K. Schultz, and A. T. Kramer. (2023). Variation in overall fitness due to seed source: Projections for predictive provenancing. *Restoration Ecology* 31: e13717.



## NOTEWORTHY COLLECTIONS

### THE REDISCOVERY OF *APHYLLON RIPARIUM* (L.T. COLLINS) A.C. SCHNEID. (OROBANCHACEAE) IN TIPPECANOE COUNTY, INDIANA, USA

Zachary Poynter

Ramboll

8845 Governor's Hill Drive, Suite 205

Cincinnati, Ohio 45249

zpoynter@ramboll.com

**Significance of the Report.** The 2019 rediscovery of *Aphyllon riparium* (L.T. Collins) A.C. Schneid. in Tippecanoe County, Indiana represents the most recent observation of the species in the county in twenty five years and its northernmost known occurrence in Indiana and the Midwest.

**Previous Knowledge.** *Aphyllon riparium* (L.T. Collins) A.C. Schneid. (Orobanchaceae) (river broomrape) was described in 2009 (as *Orobanche riparia*) as distinct from *A. ludovicianum* (Nutt) A. Gray (Collins et al. 2009). The type specimen was collected by Charles Deam in Gibson County, Indiana in 1931 (Collins et al. 2009). The New World taxa formerly included in the nearly cosmopolitan genus *Orobanche* were recently segregated into the genus *Aphyllon* (Schneider 2016), although some authorities (e.g., Weakley et al. 2017) refer some of the species, including *A. riparium*, to the genus *Myzorrhiza*, in which case the species treated here would be called *Myzorrhiza riparia* (L.T. Collins) Weakley. The name *Aphyllon riparium* is used here, however, to be consistent with recently published literature on this species (Collins et al. 2023).

*Aphyllon riparium* exhibits a wide distribution that ranges from east of the Appalachian Mountains in Virginia westward to Arizona (Collins et al. 2023), with a notable concentrated distribution in the Ohio and Wabash River Valleys (Collins et al. 2009). In *Flora of Indiana* (Deam 1940), Charles Deam indicates that it has a localized distribution in Indiana, being reported from only four counties. An observation recorded as *Orobanche ludoviciana* was made in 1939 in Tippecanoe County, Indiana (Guard and Silver 1941). It can be assumed that this is indeed *Aphyllon riparium* due to notes describing the habitat and the plants parasitizing *Ambrosia trifida* and *Xanthium strumarium*. John McCain included *Orobanche ludoviciana* Nutt. var. *ludoviciana* in his checklist of the plants of Tippecanoe County, Indiana in a 1994 report for the Sycamore Audubon Society, but no specimen exists. It is assumed that his observation was *Aphyllon riparium* due to its geographic location and the note that it was parasitizing *Ambrosia trifida*. Before the observation and collection noted in this paper, there was only one extant site known in Indiana, in Harrison County



FIGURE 1. Extant (circles) and historic (triangles) distribution of *Aphyllon riparium* in Indiana. Source of base map: GISGeography.com.

(Scott Namestnik pers. comm.). There has since been one additional observation along the White River in Morgan County, Indiana in 2022, although there is no voucher, bringing the extant distribution known in Indiana to include Harrison, Morgan, and Tippecanoe counties (Scott Namestnik, personal communication, June 2024). The historical and current distribution in Indiana thus includes Gibson, Harrison, Jefferson, Knox, Morgan, Posey, Sullivan, Tippecanoe, Warrick, and Vanderburgh counties (Figure 1).

**Discussion.** In August of 2019, Heidi Klotz Etter discovered an unidentified *Aphyllon* in a dense stand of *Ambrosia trifida* in the floodplain of the Wabash River in Prophetstown State Park in Tippecanoe County, Indiana. The author identified it as *Aphyllon riparium* in the field and notified Indiana Department of Natural Resources in addition to documenting the occurrence with iNaturalist (Figure 2) (Poynter 2021). Indiana state botanist, Scott Namestnik, visited the site in 2019 and collected a specimen that is now housed at Indiana University’s herbarium (citation below). When Scott visited to make the collection, more than 25 individuals were observed at the location with at least 50 individuals observed throughout the larger floodplain site.

The site is approximately 185 km from the nearest vouchered location in Knox County and the furthest upstream occurrence along the Wabash River. The



FIGURE 2. Flowering stems of *Aphyllon riparium* within a dense stand of giant ragweed (*Ambrosia trifida*). Photo by Zachary Poynter.

site is on well drained silty alluvium located immediately downstream from the confluence of the Tippecanoe River and the Wabash River (Figure 3). The area has been monitored by Cardno (now Stantec) from 2015 to 2023 as part of a mitigation project that includes floodplain restoration via tree/shrub planting and native seeding. The dominant cover at the site has been *Ambrosia trifida* throughout vegetation monitoring (Ryan Mendenhall, personal communication, May 2024). This site is often inundated in the early spring due to floodwaters from the Wabash River.

Since the initial 2019 observation and collection, *Aphyllon riparium* has been observed at the site in 2021 and 2022 during vegetation monitoring by Ryan Mendenhall (personal communication, May 2024). The site has had annual monitoring since 2015, but *Aphyllon riparium* was not documented until 2019. Since *A. riparium* is an annual species, it is likely that populations do not establish and flower every year. However, the plant is also relatively difficult to find in its habitat, especially if the ground layer is not observable due to vegetation being pushed down by floodwaters.



FIGURE 3. Photo showing the habitat of the specimen of *Aphyllon riparium* documented here, adjacent to a maintained walking path. Photo by Zachary Poynter.

Given the abundance of floodplain habitat that is dominated by *Ambrosia trifida* and the lack of botanists surveying such areas, this species may be overlooked. This northern observation in the Midwest suggests that this species may be found outside of its current documented range. Continued survey efforts during the flowering season should be conducted in appropriate habitats.

**Diagnostic Characters.** *Aphyllon riparium* differs from *A. ludoviciananum* in its triangular pointed corolla lobes in contrast to the rounded corolla lobes of the latter. *Aphyllon riparium* also strictly inhabits bottomlands along major rivers in either sand or silt in addition to parasitizing annual species including *Ambrosia trifida* L. and *Xanthium strumarium* L. In contrast, *Aphyllon ludoviciananum* inhabits uplands while parasitizing perennial species such as *Grindelia squarrosa* (Pursh) Dunal, *Heterotheca* spp., *Artemisia* spp., and occasionally plants in other genera. The two species also flower at different times, with *A. ludoviciananum* flowering from April to August, whereas *A. riparium* flowers from August to October.

**Specimen Citation.** INDIANA: Tippecanoe County: Prophetstown State Park, Along Trail 3, in *Ambrosia trifida*-dominated floodplain of Wabash River in clay soil. More than 25 individuals at this location, at least 50 individuals on the site. Associates include *Acer saccharinum*, *Ambrosia trifida*, *Humulus japonicus*, *Lonicera maackii*, *Persicaria longiseta*, *Phalaris arundinacea*, *Rudbeckia laciniata*, *Symphotrichum lanceolatum*, *Urtica dioica*, and *Viola sororia*. September 30, 2019, Scott Namestnik 4114 (IND) 0157531 [158532].

### ACKNOWLEDGMENTS

Thanks to Heidi Klotz Etter for her keen eye resulting in finding this population. Thanks also to Benjamin Hess who identified the area as potential habitat and who has surveyed for the species at the site previously. Ryan Mendenhall also provided general site information and history regarding the monitoring of the area. Scott Namestnik visited the population, collected the specimen referenced here, provided information on the status of the species in Indiana, and reviewed the manuscript.

### LITERATURE CITED

- Collins, L. T., A. E. L. Colwell, and G. Yatskievych. (2009). *Orobanche riparia* (Orobanchaceae), a new species from the American Midwest. *Journal of the Botanical Research Institute of Texas* 3: 3–11.
- Collins, L. T., A. C. Schneider, F. S. Coburn, and D. Von Gausig. (2023). *Aphyllon riparium* (Orobanchaceae) in Arizona. *Phytoneuron* 2023-54: 1–5.
- Deam, C. C. (1940). *Flora of Indiana*. State of Indiana Department of Conservation, Division of Forestry, Indianapolis.
- Guard, A. T. and W. H. Silver. (1942). A new station for *Orobanche ludoviciana*. *Indiana Academy of Science*. 51: 116–117. Available online at <https://journals.indianapolis.iu.edu/index.php/ias/article/view/4867/4711>
- Poynter, Z. P. (2021). iNaturalist observation: <https://www.inaturalist.org/observations/70231467>. (Accessed on May 8, 2024).
- Schneider, A. C. (2016). Resurrection of the genus *Aphyllon* for New World broomrapes (*Orobanche* s.l., Orobanchaceae). *PhytoKeys*. 75: 107–118. <https://doi.org/10.3897/phytokeys.75.10473>.
- Weakley, A. S., D. B. Poindexter, R. J. LeBlond, B. A. Sorrie, C. H. Karlsson, P. J. Williams, E. L. Bridges, et al. (2017). New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. II. *Journal of the Botanical Research Institute of Texas*. 11: 291–325.



## NOTEWORTHY COLLECTIONS

### NEW BRYOPHYTE STATE RECORD FOR WISCONSIN, USA: *PALUDELLA SQUARROSA* (HEDW.) BRID. (MEESIACEAE), TUFTED FEN MOSS

Keir Wefferling

Cofrin Center for Biodiversity  
University of Wisconsin-Green Bay  
2420 Nicolet Drive, Green Bay, WI 54311  
wefferlk@uwgb.edu

**Significance of the Report:** First collection of *Paludella squarrosa* in the State of Wisconsin.

**Previous Knowledge:** *Paludella squarrosa* (Hedw.) Brid. (Meesiaceae) (Tufted fen moss) is a circumboreal species (CBH 2024; Vitt 2014a). In North America it is relatively abundant in the Rocky Mountains and northern Cascades (Alaska south to northern Washington and Colorado, south and east to Yukon, British Columbia, and southwest Alberta), is spottily distributed throughout the central provinces and territories of Canada (Northwest Territories, Nunavut, Saskatchewan, and Manitoba), and is more abundant around the Great Lakes, Hudson Bay, and eastern Canada. In the United States it has been collected in northern New England (Maine, New York and Vermont), the upper Great Lakes region (Iowa, Michigan, Minnesota, and now Wisconsin), the middle to southern Rocky Mountains (Colorado, Montana, and Wyoming), and in Washington State. *Paludella squarrosa* is relatively abundant in Iceland and Scandinavia and occurs sporadically throughout the rest of northern Eurasia (Vitt 2014a; CBH 2024; NatureServe 2024).

**Discussion:** Within Wisconsin, *Paludella squarrosa* is known only from Oconto County in northeastern Wisconsin at Waupee Lake Swamp Research Natural Area on the Chequamegon-Nicolet National Forest. *Paludella* was found growing at the northern edge of a mineral-rich, alkaline lake on a floating sedge-peat mat bordering a white cedar swamp (or northern wet-mesic forest) near the main inlet to the lake. Waupee Lake is a calcareous groundwater-fed lake that has an unusually high number of rare and/or threatened, calcium-loving plant species (Janke 1998; Brzeskiewicz 2015; Epstein 2017). Waupee Lake Swamp is at the western edge of the largest wetland complex—including northern wet-mesic forest, lowland hardwood forest, alder thicket, northern sedge meadow, marsh communities, and “northern fen”—in the Northeast Sands Ecological Landscape (Epstein 2017).

Three specimens of *Paludella squarrosa* were collected in the boreal rich fen at Waupee Lake Swamp, either on a floating mat or on peaty soil with the fol-

lowing tracheophytes: *Amelanchier arborea* (F. Michx.) Fernald, *Andromeda glaucophylla* Link, *Calopogon tuberosus* (L.) Britton, Sterns & Poggenb., *Campanula aparinoides* Pursh, *Carex diandra* Schrank, *Carex lasiocarpa* Ehrh., *Carex magellanica* Lam., *Chamaedaphne calyculata* (L.) Moench, *Comarum palustre* L., *Cornus canadensis* L., *Cypripedium acaule* Aiton, *Cypripedium parviflorum* Salisb., *Drosera rotundifolia* L., *Eriophorum viridicarinarum* (Engelm.) Fernald, *Galium boreale* L., *Gaultheria hispidula* Dombey, *Ilex mucronata* (L.) M. Powell, Savol. & S. Andrews, *Ilex verticillata* (L.) A. Gray, *Kalmia polifolia* Wangenh., *Larix laricina* (Du Roi) K. Koch, *Menyanthes trifoliata* L., *Osmundastrum cinnamomeum* (L.) C. Presl, *Picea mariana* (Mill.) Britton, Sterns & Poggenb., *Platanthera dilatata* (Pursh) Lindl. ex L.C. Beck, *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Rubus pubescens* Raf., *Sarracenia purpurea* L., *Saxifraga pensylvanica* L., *Solidago uliginosa* Nutt., *Thelypteris palustris* Schott, *Thuja occidentalis* L., *Toxicodendron vernix* (L.) Kuntze, *Triglochin maritima* L., *Typha latifolia* L., *Vaccinium oxycoccos* L., *Vaccinium myrtilloides* Michx. The tracheophytes were identified in the field but not collected during visits to the site. Appendix 1 lists all the bryophyte species collected in association with *Paludella squarrosa* at the Waupee Lake site. Of the 23 species of co-occurring bryophytes found at Waupee Lake Swamp, 20 are county records for Oconto County (Freire et al. 2020); this brings the total number of bryophyte species recorded for the county from 128 to 148.

A number of bryophytes present at the site are considered indicator species of moderate-rich to extreme-rich fens, including *Calliergon giganteum*, *Calliergonella cuspidata*, *Campylium stellatum*, *Meesia triquetra*, *Hamatocaulis vernicosus*, *Helodium blandovii*, *Sphagnum warnstorffii*, and *Tomentypnum nitens*; tracheophyte rich fen indicators include *Carex diandra* Schrank, *Platanthera dilatata* (Pursh) Lindl. ex L.C. Beck, and *Triglochin maritima* L. (Chee and Vitt 1998; Vitt and Chee 1990). Crum and Anderson (1981) note the following bryophyte associates of *Paludella squarrosa*: *Campylium stellatum*, species of *Cinclidium* Sw., *Drepanocladus trifarius* (F. Weber & D. Mohr) Broth., *Meesia triquetra*, *Meesia uliginosa* Hedw., *Scorpidium scorpioides* (Hedw.) Limpr., and *Sphagnum warnstorffii*. Of these associates, only *Campylium stellatum*, *Meesia triquetra*, and *Sphagnum warnstorffii* have been located at Waupee Lake Swamp; *Drepanocladus trifarius*, *Meesia uliginosa*, and *Scorpidium scorpioides* are known from other rich fen sites in Wisconsin.

Ongoing searches in Wisconsin for *Paludella squarrosa* since 2021 have not yielded additional occurrences, despite repeated visits to other sites considered suitable (Epstein 2017; S. Janke, personal communication; K. Doyle, personal communication). In Wisconsin, boreal rich fen is most common along the Door Peninsula (northeastern Wisconsin), with a few additional recognized sites on the “mainland” of the state, mainly in northeastern Wisconsin (Epstein 2017). *Paludella squarrosa* is apparently quite rare in Wisconsin, although suitable habitat appears to be present in the state. According to Chee and Vitt (1990), *Paludella* is known from intermediate to extreme-rich fens, though Vitt (2014b) indicates that the species is restricted to extreme-rich fens. Though Wisconsin has other rich fen sites with several rich fen indicator species, perhaps the conditions are rarely sufficient for *Paludella* to thrive.

A review of herbarium records of *Paludella squarrosa* in the Upper Great Lakes region shows that ca. 39 vouchered specimens have been collected from approximately 26 locations in Ontario, Canada (most recently in 2013); nine vouchered specimens have been collected from approximately eight locations in three counties in Minnesota (most recently in 1984); and ca. 17 vouchered specimens have been collected from approximately ten locations in three counties in Michigan (most recently in 1974) (CBH 2024). A search of iNaturalist (2024) records from the western Great Lakes region shows six observations from Ontario, Canada, three from the single known Wisconsin site, one observation from the Lower Peninsula of Michigan, and no further observations from Minnesota.

*Paludella squarrosa* is found in calcareous wet fens in North America and Eurasia (Vitt 2014a, Jenkins 2020) and has an obligate wetland indicator status (Gillrich and Bowman 2010). Specific habitat for *P. squarrosa* has been described as wet calcareous substrates and fens in Maine (Ledlie and Allen 2019), calcareous fens in Minnesota (Leete et al. 2016), bogs and bog margins in Michigan (Mazzer and Sharp 1963), montane calcareous fens in Montana (Elliot and Pipp 2020), rich graminoid fens in New York (Slack 1992), mineral-rich fens in Vermont (Thompson et al. 2019) and montane flow-through fens dominated by graminoids in Wyoming (Heidel and Jones 2006).

**Diagnostic Characters:** *Paludella squarrosa* is a small but conspicuous dioicous acrocarpous moss 3–7 cm in height with tidy five-ranked squarrose leaves, serrulate distally, and with a luxuriant vestiture of rhizoids up the stems; the sporophytes (not seen) have setae 2.5–4.5 cm and the capsule is 2–3 mm (Vitt 2014a). As described by D. Vitt in the *Flora of North America North of Mexico*, “*Paludella* is one of the most spectacular moss species in the flora area” (Vitt 2014a). *Paludella* is described by H. Crum in *Mosses of the Great Lakes Forest*, as “one of the most attractive and curious mosses” (Crum 1983) and by Crum and Anderson (1981) as “a most curious moss, of unbelievable appearance. It is very attractive. It resembles no other moss in its densely tomentose stems and extremely squarrose-recurved leaves with the tips folded downward in such a way that they seem heart-shaped.”

**Specimen Citations:** WISCONSIN: Oconto County: 45.196543, –88.355258 at 290.5 m elevation, on a floating peat-sedge mat in a boreal rich fen at the largest inlet to Waupee Lake Swamp at the north end of the lake; September 6, 2021, *Wefferling, Berkopec, and Eicchorn 764* (UWGB). 45.196543, –88.355258 at 291 m elevation, in peaty soil in a boreal rich fen at the northwest side of Waupee Lake; June 17, 2022, *Wefferling and Smith 851* (UWGB). 45.196514, –88.355254 at 291 m elevation, in peaty soil in a boreal rich fen at the northwest side of Waupee Lake; June 17, 2022, *Wefferling and Smith 861* (UWGB).

#### ACKNOWLEDGMENTS

This work would not have been possible without permission and logistical support from the United States Forest Service (USFS) offices; I gratefully acknowledge permission to access and collect plant specimens within the Waupee Lake Swamp Research Natural Area on the Chequamegon-Nicolet National Forest (CNNF), facilitated by Ann Dassow, Heather Jensen, Christel Kern, Susan Krage, Allie Niemeyer, Linda Parker, and Ryan Vinhal. Collections and observations at the site were

performed with the help of Sarah Baughman, Joan Berkopec, Ron Eicchorn, Nicholas Gabbard, Jason Miller, and Al Powell. Funding comes from the Wisconsin Coastal Management Program, grant number AD239125 – 024.02 and an American Philosophical Society Franklin Research Grant. Justin J. Bournoville (CNNF) provided extensive details resulting from a literature search on the taxon when preparing a USFS Risk Assessment report. Steve Janke (also CNNF) shared valuable information regarding habitat quality and history of the site, and Kevin Doyle (Wisconsin Department of Natural Resources, Natural Heritage Inventory) has shared useful insights into potential indicator species and additional sites to search. Emmet Judziewicz (University of Wisconsin, Stevens Point) and an anonymous reviewer provided helpful reviews of an earlier draft of the manuscript, and Michael Huft (Editor, The Great Lakes Botanist) provided careful editing and additional helpful comments that greatly improved the paper.

### LITERATURE CITED

- Brzeskiewicz, M. E. (2015). Establishment Record for Waupee Lake Swamp Research Natural Area, Chequamegon-Nicolet National Forest, Lakewood-Laona District, Oconto County, Wisconsin. Rhinelander, Wisconsin: USDA, Forest Service, Chequamegon-Nicolet National Forest.
- Chee, W.-L., and D. H. Vitt. (1998). The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in Central Alberta, Canada. *Wetlands* 9: 227–261.
- CBH (2024). Consortium of bryophyte herbaria. Occurrence records for *Paludella squarrosa*. CBH Portal [web application]. Available at <https://bryophyteportal.org/portal/>. (Accessed September 19, 2024).
- Crum, H. A. (1983). Mosses of the Great Lakes forest. University of Michigan, Ann Arbor.
- Crum, H. A., and L. E. Anderson. (1981). Mosses of eastern North America, Volume 1. Columbia University Press, New York, N.Y.
- Elliot J. C., and A. K. Pipp. (2020). A checklist of Montana mosses (1880–2018). Helena, Montana: Montana Natural Heritage Program.
- Epstein, E. E. (2017). Natural communities, aquatic features, and selected habitats of Wisconsin. Chapter 7 in *The ecological landscapes of Wisconsin: An assessment of ecological resources and a guide to planning sustainable management*. PUB- SS-1131H 2017. Wisconsin Department of Natural Resources, Madison.
- Freire, A. V., E. J. Judziewicz, and F. Bowers (2020). Bryophytes of Butternut Pines, Oconto County, Wisconsin. *The Great Lakes Botanist* 59: 178–190.
- Gillrich J. J., and K. C. Bowman. (2010). The use of bryophytes as indicators of hydric soils and wetland hydrology during wetland delineations in the United States ERDC/CRREL TR-10-9. U.S. Army Corps of Engineers, Engineer Research and Development Center, Hanover, New Hampshire.
- Heidel, B., and G. Jones. (2006). Botanical and ecological characteristics of fens in the Medicine Bow Mountains, Medicine Bow National Forest, Albany and Carbon Counties, Wyoming. FS Agreement No. 02-CS-11020600-033 M8. Wyoming Natural Diversity Database, University of Wyoming, Laramie.
- iNaturalist. (2024). Available at <https://www.inaturalist.org>. (Accessed September 19 2024).
- Janke, S. (1998). Chequamegon-Nicolet National Forest Research Natural Area evaluation report: Waupee Lake. Unpublished reports on file in Park Falls Headquarters.
- Jenkins, J. (2020). Mosses of the northern forest: A photographic guide. Cornell University Press, Ithaca, New York.
- Ledlie, P., and B. Allen. (2019). Maine Mosses: County Checklist. *Rhodora* 121: 297–327.
- Leete, J. H., W. R. Smith, J. A. Janssens, and N. Aaseng. (2016). Technical criteria for identifying calcareous fens in Minnesota. Excerpted from Final report to the U.S. EPA: Test of the technical criteria for identifying and delineating calcareous fens in Minnesota and draft revised technical criteria for identifying calcareous fens in Minnesota, 2005. Minnesota Department of Natural Resources, St. Paul.
- Mazzer, S. J., and A. J. Sharp. (1963). Some moss reports for Michigan. *The Bryologist* 66: 68–69.
- NatureServe. (2024). Comprehensive report for *Paludella squarrosa*. NatureServe Explorer [web application]. NatureServe, Arlington, Virginia. Available at [https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.127491/Paludella\\_squarrosa](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.127491/Paludella_squarrosa). (Accessed September 19, 2024).

- Slack, N. G. (1992). Rare and endangered bryophytes in New York State and eastern United States: Current status and preservation strategies. *Biological Conservation* 59: 233–241.
- Thompson, E. H., E. R. Sorenson, and R. J. Zaino. (2019). *Wetland, woodland, wildland: A guide to the natural communities of Vermont*, second edition. Vermont Fish and Wildlife Department, Montpelier.
- Vitt, D. H. (2014a). *Paludella*, P. 34 in *Flora of North America*, Volume 28: Bryophyta, part 2, *Flora of North America* Editorial Committee, editors. Oxford University Press, New York, N.Y.
- Vitt, D. H. (2014b). A key and review of bryophytes common in North American peatlands. *Evansia* 31: 121–158.
- Vitt, D. H., and W.-L. Chee (1990). The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89: 87–106.

APPENDIX 1. Bryophyte vouchers collected in a boreal rich fen at Waupee Lake Swamp Research Natural Area. All were collected by Keir Wefferling and colleagues at the north end of Waupee Lake near 45.1964, –88.3554, ca. 290m elevation and deposited at UWGB. Species that are county records for Oconto County are marked with an asterisk (\*).

- 
- \**Aulacomnium palustre* (Hedw.) Schwägr., *Wefferling and Gabbard* 1012 (August 11, 2022)
- \**Calliergon giganteum* (Schimp.) Kindb., *Wefferling and Miller* 866 (June 17, 2022)
- \**Calliergonella cuspidate* Loeske, *Wefferling and Miller* 854 (June 17, 2022), *Wefferling and Gabbard* 1009 (August 11, 2022), *Wefferling and Gabbard* 1014 (August 11, 2022)
- \**Campylium stellatum* (Hedw.) C.E.O. Jensen, *Wefferling and Gabbard* 1013 (August 11, 2022)
- \**Drepanocladus aduncus* (Hedw.) Warnst., *Wefferling and Miller* 845 (June 17, 2022)
- Fuscocephaloziopsis lunulifolia* (Dumort.) Váňa & L. Söderstr., *Wefferling and Gabbard* 1016 (August 11, 2022), *Wefferling and Gabbard* 1029 (August 11, 2022)
- \**Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Wefferling, Berkopec, and Eicchorn* 766 (September 6, 2021), *Wefferling and Miller* 852 (June 17, 2022)
- \**Helodium blandovii* (F. Weber & D. Mohr) Warnst., *Wefferling, Berkopec, and Eicchorn* 765 (September 6, 2021), *Wefferling and Miller* 869 (June 17, 2022), *Wefferling and Gabbard* 1018 (August 11, 2022)
- \**Meesia triquetra* (Richt.) Ångstr., *Wefferling and Miller* 873 (June 17, 2022), *Wefferling, Baughman, and Powell* 1820 (June 7, 2024)
- \**Paludella squarrosa* (Hedw.) Brid., *Wefferling, Berkopec, and Eicchorn* 764 (September 6, 2021), *Wefferling and Miller* 851 (June 17, 2022), *Wefferling and Miller* 861 (June 17, 2022)
- Polytrichum strictum* Bridel, J. Bot. (Schrader), *Wefferling and Miller* 871 (June 17, 2022), *Wefferling and Miller* 872 (June 17, 2022), *Wefferling and Gabbard* 1011 (August 11, 2022)
- \**Riccardia multifida* (L.) Gray, *Wefferling and Gabbard* 1015 (August 11, 2022)
- \**Sphagnum capillifolium* (Ehrh.) Hedw., *Wefferling, Berkopec, and Eicchorn* 754 (September 6, 2021), *Wefferling, Berkopec, and Eicchorn* 755 (September 6, 2021), *Wefferling and Miller* 850 (June 17, 2022)
- \**Sphagnum centrale* C.E.O. Jensen, *Wefferling and Gabbard* 1030 (August 11, 2022)
- \**Sphagnum contortum* Schultz, *Wefferling and Gabbard* 1034.1 (August 11, 2022), *Wefferling and Gabbard* 1034.2 (August 11, 2022)
- \**Sphagnum divinum* Flatberg & K. Hassel, *Wefferling, Berkopec, and Eicchorn* 753 (September 6, 2021), *Wefferling, Berkopec, and Eicchorn* 756 (September 6, 2021), *Wefferling and Miller* 849 (June 17, 2022), *Wefferling and Gabbard* 1007 (August 11, 2022)
- \**Sphagnum fuscum* (Schimp.) H. Klinggr., *Wefferling, Berkopec, and Eicchorn* 762 (September 6, 2021), *Wefferling and Gabbard* 1022 (August 11, 2022), *Wefferling and Gabbard* 1023 (August 11, 2022)
- \**Sphagnum girgensohnii* Russow, *Wefferling, Berkopec, and Eicchorn* 751 (September 6, 2021), *Wefferling, Berkopec, and Eicchorn* 760 (September 6, 2021), *Wefferling and Gabbard* 1033 (August 11, 2022)
- Sphagnum russowii* Warnst., *Wefferling and Gabbard* 1021 (August 11, 2022)
- \**Sphagnum squarrosum* Crome, *Wefferling and Miller* 864 (June 17, 2022), *Wefferling and Gabbard* 1027 (August 11, 2022), *Wefferling and Gabbard* 1028 (August 11, 2022)



---

\**Sphagnum teres* (Schimp.) Ångstr. ex C. Hartm., *Wefferling and Gabbard 1008* (August 11, 2022),  
*Wefferling and Miller 1819* (June 7, 2024)  
\**Sphagnum warnstorffii* Russow, *Wefferling, Berkopec, and Eicchorn 768* (September 6, 2021), *Wef-*  
*ferling and Miller 863* (June 17, 2022)  
\**Tomentypnum nitens* (Hedw.) Loeske, *Wefferling and Gabbard 1006* (August 11, 2022)

---

## BOOK REVIEW

**Robin Wall Kimmerer. 2013. *Braiding Sweetgrass: Indigenous Wisdom, Scientific Knowledge, and the Teachings of Plants*. Milkweed Editions, Minneapolis, Minnesota. xii + 390 pp. hardcover \$35.00. ISBN 978-1-57131-335-5. Paperback \$20.00. ISBN 978-1-57131-356-0. eBook \$9.00 ISBN 978-1-57131-871-8.**

The national bestseller *Braiding Sweetgrass* is an inspiring exploration of the relationship between humans and nature as seen by indigenous people of the Great Lakes area. The deep acknowledgment in indigenous traditions of our absolute dependence on plants, animals, and the earth itself is vividly portrayed in the stories, rituals, and indigenous wisdom that are recounted in this book.

The book begins with a moving illustration of this complete dependence: an account of the creation of humanity that is widespread among native peoples in the Great Lakes area. In the beginning, water covered the Earth, and there were no humans. But one day the animals of the Earth saw a woman, Skywoman, falling from the sky, heading for the dark water. The geese, ducks, fish, beavers, otters, muskrats, and other animals noted her approach and conferred among themselves on how to save her from drowning when she landed. Through the cooperation of the animals, she was able to stand on a turtle. A courageous muskrat brought up mud from the bottom of the ocean that allowed Skywoman to produce land on the turtle's back. This formed what is widely called "Turtle Island" among indigenous peoples in the Midwest. Skywoman also brought seeds of all the plants with her, scattering them on the new Earth. One version of this account says that sweetgrass, *Hierochloe odorata*, was the first plant to grow. Skywoman, who was pregnant, began the peopling of the Earth, and gave instructions to these new inhabitants for correct ways of living.

Why the emphasis on sweetgrass? Sweetgrass is considered the hair of Mother Earth. It is tended and carefully harvested. Braids of dried sweetgrass are made to signify care for the earth's well-being, are given as gifts signaling gratitude and kindness, and are burned for ceremonial healing. In *Braiding Sweetgrass*, Robin Wall Kimmerer braids indigenous plant knowledge, scientific knowledge, and an account of her life as a plant scientist strongly identified with her native Anishinabekwe heritage into a cord of scientific plant lore and reflections on indigenous ways of knowing. This cord affirms our potential to heal the earth by learning from indigenous wisdom. She demonstrates the power of themes derived from the first instructions given to humans to transform the frequently destructive European narrative of Man as the conqueror of Earth and, all too often, its destroyer. As habitat elimination and climate change become more threatening to us and to the plants and animals we rely on, Kimmerer's 2013 book becomes ever more relevant to our outlook on the world.

Kimmerer, who has a PhD in plant ecology from the University of Wisconsin-Madison, is enrolled in the Citizen Potawatomi Nation. She is a MacArthur Fel-

low. She is currently on the faculty of the State University of New York College of Environmental Science and Forestry. She teaches botany, ecology, ethnobotany, and other courses in a model incorporating scientific data, hands-on experience, and traditional ecological knowledge (TEK). TEK is a synthesis of the ways of knowing and living in interdependence with the earth that have been practiced by indigenous peoples throughout the world. Kimmerer has also worked to promote access to scientific learning and careers for indigenous students.

Most of the 31 chapters in *Braiding Sweetgrass* are organized around a one or a few plant species: strawberries, wild rice, maples, black ash, silverbells, and witch hazel, among others that will be familiar to Great Lakes botanists. Each chapter includes traditional knowledge and philosophy about a plant or a natural process, generally from the Anishinaabe culture, as well as fascinating scientific information.

In a chapter on the indigenous concept of plants and animals as persons, for example, Kimmerer discusses how she collects wild leeks as medicinal food in the spring. When she goes to harvest leek bulbs, she ceremonially asks their permission for the harvest. Asking permission acknowledges that we depend totally on plants and animals, as equal inhabitants of the earth, to generously sacrifice their bodies for our nutrition. Asking permission also entails assessing the health of the individual leeks and of their populations at an intuitive level as well as a rational level.

The collector needs to sense when the leeks are ready to harvest, and how intense the harvest can be without compromising the future of the leek population. Caring for the long-term health of the leek population may sometimes call the harvester to restrict their harvest and at other times to mindfully thin overcrowded sections of the leek patch. Comprehensive care for the leeks both sustains the harvestable food source and also acknowledges the obligation we have to these beings because of their sacrifices on our behalf. This blend of leek biology with indigenous ethics is typical of Kimmerer's work in *Braiding Sweetgrass* and makes for engrossing and educational reading.

Some chapters deal more directly with the philosophy of traditional ecological knowledge. One chapter focuses on the Haudenosaunee (Iroquois) Thanksgiving Address. The Thanksgiving Address is a central prayer of this tradition that is said in schools and at social, cultural and other events. It systematically thanks all elements of the natural world for their contributions to maintaining humanity and the functioning of the earth. Water, fish, food plants, medicinal herbs, trees, mammals, birds, the wind and the other elements of the world are acknowledged and thanked. The specific contributions of each are included in the Address in brief form, so that all who recite it are reminded of the source of what sustains us. Incorporating real gratitude and a strong sense of reciprocity toward the natural world and the other beings in it is central to indigenous philosophy. Asking leeks for permission to harvest them is just one application of this sense of gratitude.

Botanists are sometimes told to avoid anthropomorphizing plants—informally talking about them as if they have some level of cognition or intent. Asking a leek patch for permission to harvest it would seem, in one sense, to grossly

anthropomorphize it. Leeks certainly do not hear or realize this request. But perhaps the profound sense of gratitude and reciprocity toward the natural world expressed in *Braiding Sweetgrass* is not so much about thinking that leek plants are listening to us, as it is about augmenting our ability to listen to, or pay detailed attention to, the needs of leeks and other plants and animals.

We need to better listen to nature, that is, to heed the increasingly desperate signals being sent out by so many aspects of the natural world, so that we can better serve and care for it as it has always cared for us. Steeping yourself in indigenous ecological knowledge and philosophy through reading Kimmerer's book is a potent way to allow this worldview to expand your own thinking. The volume is enthusiastically recommended to all Great Lakes botanists.

——Charlotte Gyllenhaal  
University of Illinois Chicago  
and Block Center for Integrative Cancer Treatment  
cgyllenhaal@gmail.com